TEMPORAL AND SPATIAL TRENDS IN DRILLING PREDATION ON *CREPIDULA* IN THE U.S. COASTAL PLAIN

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A Thesis Submitted to the
University of North Carolina at Wilmington in Partial Fulfillment
Of the Requirements for the Degree of
Master of Science

Department of Earth Sciences

University of North Carolina at Wilmington

2003

Approved by

Advisory Committee

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ABSTRACT

A comprehensive study of drilling predation by naticid and muricid gastropods on prey species belonging to the gastropod genus *Crepidula* was conducted for Plio-Pleistocene mollusc assemblages from the Atlantic Coastal Plain of Virginia, North Carolina, and South Carolina, and from the Atlantic and Gulf Coastal Plain of Florida. Muricid and naticid drilling frequencies in the study area steadily decreased from the middle Pliocene to the late Pliocene and then rose significantly into the Pleistocene, following the Plio-Pleistocene mass extinction. Spatial comparisons of drilling frequencies revealed that drilling predation was more intense in higher latitudes than in lower latitudes. Drilling frequencies on *Crepidula* were inversely correlated with prey effectiveness (the ratio of incomplete drillholes to total attempted drillholes). Prey effectiveness gradually increased in the Pliocene and decreased significantly following the Plio-Pleistocene extinction. Prey effectiveness was generally higher in lower latitudes than in higher latitudes. Temporal and spatial trends in predation intensity and prey effectiveness appear to be influenced by competition. Low drilling frequencies and high prey effectiveness were correlated with intense competition because competition increases the likelihood of drilling being interrupted. Muricids and naticids were highly selective with respect to drillhole site on the prey's shell for Pliocene and Pleistocene samples in both of the study areas. Predator-prey interaction between drilling muricid and naticid gastropods and the gastropod genus *Crepidula* provided some evidence for escalation, but did not support coevolution.

# ACKNOWLEDGMENTS

I would like to thank Dr. Michael Rischbieter for getting me interested in evolutionary biology and paleontology, and for encouraging me to pursue a higher education in earth sciences. Thanks go to Dr. Lynn Leonard for referring me to my advisor, and for making sure I received financial support to continue. I would also like to thank my advisor Dr. Patricia Kelley for accepting me and giving me this opportunity. I also want to thank Tricia for being such a good advisor and taking time out of her busy schedule to help me out no matter the circumstance. Thanks go to my committee members, Dr. Jack Hall and Dr. Richard Laws, for their patience and helpful suggestions throughout my project. Special thanks go to Dr. Greg Dietl for his guidance and help along the way. Also, thanks go to the rest of the faculty for helping me get the most out of my education. Special thanks go to Cathy Morris for all those times she went out of her way to help me out, I couldn't have done it without you.

I would like to thank my mother and father for always being there for me and making my life so enjoyable. You really are the greatest parents in the world. I also want to thank my brother Bryan for just being himself. I can't put into words how important you have been in my life. I also want to thank my older brother and sister, Chas and Kem, and their families for their continued support.

Thanks go to all fellow students and friends who have made me enjoy my time here in Wilmington. I would especially like to thank Ansley for her continuous patience and support over the past year. I especially want to thank Ansley for being there for me and helping me through all the difficulties of these past few months; there is no way I could have done this without you.

Thanks go to the Department of Earth Sciences, Geological Society of America, Southeastern GSA, and Sigma Xi for providing financial support for this project. I also want to thank Roger Portell, Buck Ward, Greg Herbert, and Dr. Ed Petuch for helping me get the samples for this project.

## DEDICATION

I would like to dedicate this thesis to my grandfather, Clinton Heyward Morgan, whose generosity, kindness, and love for family taught me the important things in life.

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# INTRODUCTION

## Evolutionary Concepts

The idea of natural selection as a mechanism for evolution was proposed by Charles Darwin (1872) in his book *The Origin of Species*. Darwin suggested that slow gradual changes in earth processes cause similar changes in community structure (Jackson et al. 1996). Conditions on earth have continued to change through time and these changes have caused species to either adapt to such changes or migrate to an area more suitable for survival. Species that are unable to adapt or migrate go extinct and a new or immigrant taxonomic group rapidly fills their niche space. The origination, migration, adaptation, and extinction of species through time and space have been continually reshaping communities since the origin of life. For more than a century scientists viewed evolution as a slow, gradual process in which new species evolve through continuous adaptations within populations in response to gradually changing environmental conditions. Eldredge and Gould (1972) challenged the theory of gradualism by proposing the hypothesis of punctuated equilibrium. According to this hypothesis species evolve and establish stable populations that exhibit little, if any, change for an extended period of time. When species do undergo change it occurs rapidly and is concentrated during times of speciation (Vermeij, 1987). These rapid speciation events are often brought on by sudden changes in the environment, causing multiple lineages within a community to go extinct. However, some species are able to adapt to these abrupt changes and rapidly accumulate numerous adaptive traits, causing the lineage to split, resulting in a new species (Vermeij, 1987). The only direct evidence that can be used to study long-term evolution is the fossil record. Therefore, knowledge of evolutionary change and speciation is based on the morphology of fossil taxa.

Many studies have provided evidence for gradual evolution, while other studies have supported punctuated equilibrium. Studies supporting gradualism show continuous, directional morphologic change within a lineage through time. Lineages that show punctuated equilibrium exhibit a period of long-term stasis and short-term morphologic change concentrated during times of speciation (Eldredge and Gould, 1972). The fossil record provides evidence for morphologic stability, but many argue that these studies are based on marine benthic species from time-averaged stratigraphic sections (Vermeij, 1987). Samples used to support stasis represent long time intervals and are more prone to processes of sediment disturbance increasing the likelihood that morphologic stability is the result of preservational and sampling bias rather than real evolutionary processes (Vermeij, 1987). Fossils used to support gradualism are usually taken from stratigraphic sections that exhibit little, if any, gaps because they are usually taken from environments where sedimentation occurs at a faster, more continuous rate, and represent shorter time intervals than most of the samples used to support stasis. Gould (1985) argued that most studies supporting gradualism do not incorporate mass extinctions, which are likely to undo any gradual evolutionary trends that have accumulated within local communities over a relatively short time period. The fossil record provides supporting evidence for both punctuated equilibrium and gradual evolution, which suggests that both evolutionary processes have helped shape life on earth.

Species within a community respond differently to local environmental changes as well as fluctuations in competition and predation, resulting in a constant restructuring of communities through time. Abiotic and biotic forces acting on organisms within a community usually result in an evolutionary progression of species that are fit for that particular environment. Gould (1985) referred to these as “evolutionary events of the first tier,” and said they represent an “ecologic moment” in geologic time. Gould (1985) argued that forces of the first tier may result in evolutionary trends at the species level, or within a population, but these trends are eventually eliminated by large-scale events, such as a mass extinction. Mass extinction events cause rapid environmental changes across a broad geographic area, resulting in a massive extinction of organisms above the genus level. Lineages that survive do so by chance and rapidly fill open niche space, restarting the evolutionary process (Eldredge and Gould, 1972). The view of mass extinctions undoing species-level trends questions the role of ecologic interaction in evolution

(Gould, 1985; Allmon, 1992). This view assumes that the adaptations a lineage has accumulated in response to changes in competition, predation, and the physical environment have no bearing on whether or not that lineage survives a mass extinction.

Modern studies in evolution are focusing on various aspects of ecological interaction, and trying to determine if ecology plays a significant role in tempo and mode of evolution. Studies of predator-prey systems address the role of ecologic interaction in evolution (Kelley and Hansen, 2001). Naticids and muricids are drilling gastropods that have been used commonly in predator-prey studies. Vermeij (1987) proposed that the interaction between drilling gastropods and their prey through time has been characterized by escalation. The hypothesis of escalation states that biological hazards, such as predation, and adaptations to such hazards have increased through time, producing long-term trends in the morphology, behavior, and distribution of organisms (Vermeij, 1987). Predator-prey systems have also been used to support the hypothesis of coevolution (Dietl and Alexander, 2000; Kitchell, 1982). Coevolution is a reciprocal relationship between predator and prey in which prey respond to predators by evolving antipredatory characteristics, causing predators to increase their predatory capabilities (Kelley and Hansen, 2001; Futuyma and Slatkin, 1983). The difference between coevolution and escalation is that coevolution involves the accumulation of adaptations of both the predator and the prey in response to each other, while escalation involves the accumulation of adaptations of the prey in response to their enemies, and though the predators may adapt better offensive capabilities, they are more likely to respond to their own enemies rather than adapt to their prey's defensive strategies (Kelley and Hansen, 2001).

Various studies of the naticid gastropod predator-prey system have been interpreted as providing evidence for either coevolution or escalation (Kelley and Hansen, 1993, 1996a; Dietl and Alexander, 2000; Vermeij, 1994). Furthermore, these studies have shown that evolution of the naticid predator-prey system may result in gradual change, punctuation, or stasis depending on various physical, biological, and chemical conditions acting on the system at that particular time and place (DeAngelis et al., 1985; Vermeij, 1987, 1994). DeAngelis et al. (1985) concluded from mathematical models that the pace at which predator-prey coevolution occurs depends on several aspects such as predation intensity, relative size of the predator and prey, prey defensive strategies, and predator offensive capabilities. The tempo at which escalation occurs depends on the taxonomic level that is being analyzed. Vermeij (1987, 1994) suggested that escalation at the faunal level has been episodic, brought on by climate change, an increase or decrease in nutrient supply, and/or sea-level change. However, the pace at which escalation occurs within a lineage is uncertain and depends on the adaptive capabilities of a species with regards to environmental change, as well as changes in competition and predation (Vermeij, 1987; Kelley and Hansen, 2001).

Previous studies conducted by Kelley and Hansen (1996, 2001, 2003) on naticid gastropod predation of molluscan faunas have revealed patterns of escalation that were influenced by mass extinction events. Kelley and Hansen (1996, 2001, 2003) calculated naticid drilling frequencies on more than 150,000 bivalve and gastropod specimens from bulk samples of Cretaceous through Recent age (28 formations, 24 stratigraphic levels from the Atlantic and Gulf Coastal Plains). Their data showed that naticid drilling frequencies rose significantly in recovery faunas following mass extinction events (Figure 1). Mass extinctions reshape faunal structure, and can be attributed to changes in the physical environment. Therefore, the pace of escalation at the faunal level appears to be triggered by changes in the physical environment, and is probably not a result of predator-prey interaction acting alone. Most species within a given fauna respond differently with regard to fluctuations in the environment, competition, and predation. Studies supporting escalation and coevolution are primarily concerned with adaptations that have accumulated through predator-prey interaction. It might be easier to determine if adaptations are a direct result of predator-prey interaction by narrowing a study to a single prey lineage that has a relatively broad geographic and geologic range, and is abundant in the fossil record. Fossil lineages that

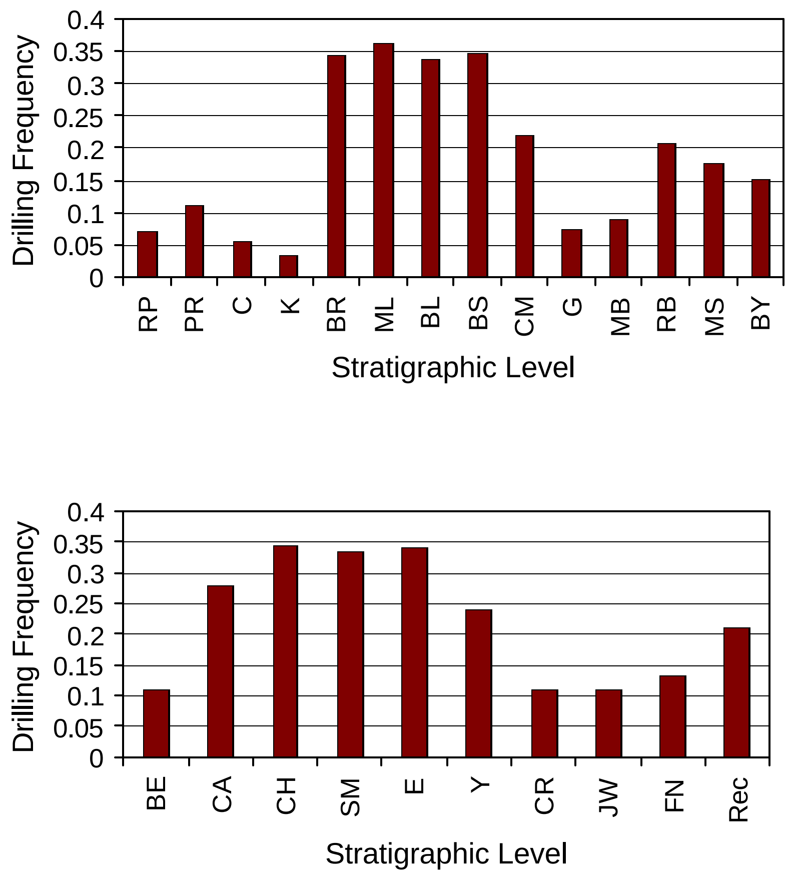


Figure 1. Naticid drilling frequencies for the entire molluscan fauna (bivalves + gastropods) from Kelley-Hansen (2003) database on naticid predation in the Gulf and Atlantic Coastal Plain. Top: Cretaceous through Paleogene; bottom, Neogene through Recent. Stratigraphic units: Cretaceous: RP, Ripley Fm; PR, Providence Fm; C, Corsicana Fm. Paleocene: K, Kincaid Fm; BR, Brightseat Fm; ML, Matthews Landing Mbr of Naheola Fm; BL, Bells Landing Mbr of Tuscahoma Fm. Eocene: BS, Bashi Mbr of Hatchetigbee Fm; CM, Cook Mountain, Upper Lisbon, and Piney Point Fms; G, Gosport Fm; MB, Moodys Branch Fm. Oligocene: RB, Red Bluff Fm; MS, Mint Spring Fm; BY, Byram Fm. Latest Oligocene/Early Miocene: BE, Belgrade Fm. Miocene: CA, Calvert Fm; CH, Choptank Fm; SM, St. Marys Fm; E, Eastover Fm. Pliocene: Y, Yorktown Fm; CR, Chowan River Fm. Pleistocene: JW, James City and Waccamaw Fms; FN, Flanner Beach and Neuse Fms. Rec, Recent.

meet these criteria can be analyzed with precision, and abiotic and/or biotic forces causing morphologic change can be more accurately determined and correlated with better resolution than within a total fauna. The gastropod genus *Crepidula* is an ideal lineage to study predator-prey interaction because of its wide geographic distribution, as well as its persistence and abundance in the fossil record.

Muricid vs. Naticid Gastropods

Naticids and muricids have been shell-drilling predators of molluscs since the Cretaceous (Kelley and Hansen, 1996). These two drilling gastropods differ in several aspects. Muricids are epifaunal organisms that generally feed above the surface of the sediment (Reyment, 1967). Naticids are infaunal predators that usually feed just beneath the sediment surface (Reyment, 1967; Kabat, 1990; Carriker, 1981). Previous studies on muricids have shown that these gastropods sometimes feed in groups (Brown & Alexander, 1994). Group foraging has not been shown to be a common feeding strategy in naticids because naticids wrap their entire foot around their victims, leaving little if any portion of their prey exposed. Studies have also indicated that if a muricid is dislodged while drilling, it is able to relocate the drill site and continue the process; in contrast, if a naticid is dislodged then it usually restarts the process at a different site on the prey shell (Reyment, 1967). Muricids drill steep-sided, cylindrical holes that are sometimes slightly countersunk, while naticid boreholes are parabolic and usually are markedly countersunk (Guerrero & Reyment, 1988; Carriker, 1981). Naticid boreholes are generally larger than muricid boreholes due to the fact that most extant naticids are larger in size than muricids. The differences in the morphology of muricid and naticid boreholes are used to distinguish between the two in the fossil record, although similarities in borehole morphology among certain groups of muricids and naticids as well as taphonomy can sometimes make this distinction difficult.

Herbert and Dietl (2002) have shown that similarities in borehole morphology exist between the naticid predator, *Neverita duplicata*, and the muricid predators, *Chicoreus dilectus* and *Phyllonotus pomum*, in the bivalve prey *Chione elevata*. Their results suggest that previous results based on drillholes in *Chione* may be biased due to predator misidentifications (Herbert and Dietl, 2002). Taphonomy may also cause similarities between muricid and naticid boreholes, especially for small, thin-shelled prey specimens (Kowalewski, 1993). Erosion and dissolution along the perimeter of the borehole removes distinguishing characteristics left by the predator, sometimes making it difficult to determine if the borehole was muricid or naticid in origin.

Several other groups of molluscs have been discovered to drill holes that are similar to those made by naticids and muricids (Harper et al., 1998). Some members of the Nassariidae drill naticid-like holes, but usually appear to be slightly more irregular than naticid holes (Morton and Chan, 1997). Members of the Marginellidae have also been reported to drill naticid-like holes, but also make holes resembling those drilled by octopods (Ponder and Taylor, 1992; Carriker and Gruber, 1999). Certain octopods and buccinids sometimes drill holes similar to muricids (Peterson and Black, 1995). Similarities in drillhole morphology between muricids, naticids, and several other groups of molluscs are not very common, but when such cases do exist, a drillhole usually can be distinguished based on the location of the drillhole, the type of prey that was drilled, and the abundance of muricids and naticids within the fauna (Kelley and Hansen, 2003).

The process of shell penetration is fairly similar in muricids and naticids in that both groups of drilling gastropods penetrate their prey's shell using an accessory boring organ (ABO) and a radula (Carriker, 1981). However, the ABO is located in three separate anatomical regions of naticids and muricids (Carriker, 1981). The ABO in all naticids is located on the anterior ventral lip of the proboscis. The ABO in all muricid males and most females is located in the mid-anterior ventral part of the foot; however, the ABO in females lies anterior to the ventral pedal gland (VPG). In females of several species of muricids (*Purpura clavigera, Rapana thomasiana, Thais haemastoma, T. haemastoma floridana,* and *T. haemastoma canaliculata)* the ABO lies atop the VPG, so that during eversion it passes through the cavity of the VPG.

Although the mechanism of shell penetration is fairly similar in naticid and muricid gastropods, there are slight differences in the rasping techniques of the two groups. The differences in borehole morphology between muricids and naticids can be attributed to their slight differences in rasping their prey's shell. In muricids, rasping is concentrated towards the bottom of the incomplete borehole (Carriker, 1981). Rasping by the radula is uniformly firm, and covers the entire surface of the borehole (Carriker, 1981). This produces a straight-sided, cylindrical borehole that is characteristic of most species of muricid gastropods (Figure 2a). In naticids rasping is done systematically beginning at the center of the incomplete borehole and extending out to the periphery (Carriker, 1981). The least amount of rasping occurs at the center of the borehole, thus resulting in a markedly countersunk borehole that is typical of most naticid species (Figure 2b).

History of *Crepidula*

The genus *Crepidula* is one branch of a group of mesogastropods that radiated into ecological space that was formerly dominated by epifaunal bivalves (Hoagland, 1977). *Crepidula* species are well represented in many shallow-water faunas ranging from cold temperate climates to the tropics (Hoagland, 1977). Fossils indicate that the genus *Crepidula* evolved in the mid to late Cretaceous at which time they occurred in small, sparsely scattered populations (Hoagland, 1977). The genus *Crepidula* experienced massive expansion and radiation throughout the Paleocene and Eocene. By the Miocene, *Crepidula* populations were geographically widespread, occupying numerous climates (Hoagland, 1977). As a whole, *Crepidula* species have changed very little since the Miocene, and most fossil species are indistinguishable from modern representatives (Hoagland, 1977). However, there have been morphologic changes in degree of species variability for many *Crepidula* species (Hoagland, 1977). Forty species are recognized from the fossil record worldwide, of which only one-fourth are known to be extinct (Hoagland, 1977).

*Crepidula* are sedentary, filter-feeding organisms that colonize by attaching to firm substrates. Substrates can include anything from rocks to hard bottoms to living whelks. Some species of *Crepidula* colonize a substrate by forming dense populations of stacked individuals. Most

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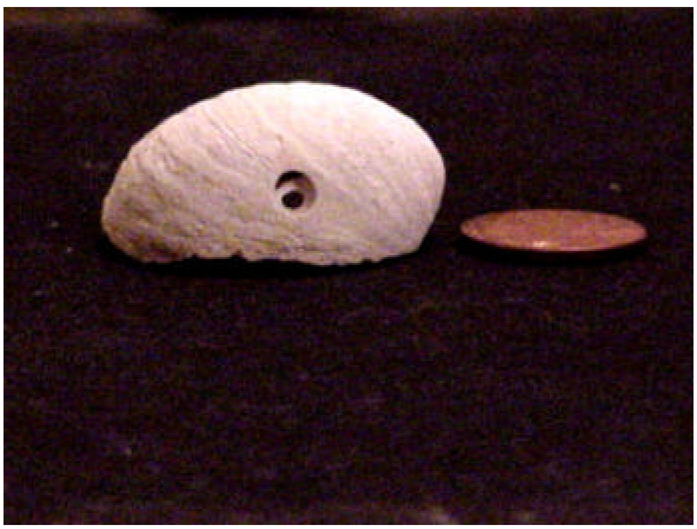
b. 

Figure 2.  a.)  Specimen of *C. fornicata* with a straight-sided cylindrical muricid drillhole.

b.)  Specimen of *C. fornicata* with a countersunk naticid drillhole.

*Crepidula* species are considered generalists with regards to variations in temperature and salinity, which has enabled them to inhabit many different types of environments, including unstable environments (Hoagland, 1977). All species of *Crepidula* brood their young during early development; however, some species produce few offspring, retaining their young until they develop into crawling stages, while others produce many offspring and release them as planktotrophic larvae (Hoagland, 1977). Speciation within the genus *Crepidula* is favored by species with non-pelagic larvae because they are good at forming peripheral isolates necessary for speciation to occur (Hoagland, 1977). However, these species are poor long distance colonizers, thus confining their geographic distribution and limiting their environmental tolerance. Species with planktotrophic larvae are good long-distance colonizers, and are geographically widespread, thus allowing them to adapt to environmental changes, which often leads to variability between populations of a species (Hoagland, 1977).

The success of the genus *Crepidula* might be somewhat unpredictable because of its sedentary lifestyle, which drastically reduces any possible escape from predation and limits their ability to migrate. *Crepidula* species have overcome these barriers by utilizing other means of survival. The success of this genus can be attributed to the combination of stacking and brooding by certain species, which enhances survivorship because this type of life habit and reproductive mode reduces the number of individuals exposed to predation, and increases the percentage of individuals that reproduce. Most molluscan prey are incapable of defending themselves against predators, particularly drilling gastropods (Carriker, 1981). An exception is *Crepidula fornicata*, which fends off a predator by jabbing it with its radula, or dislodges the predator from its valve by pressing it against an obstacle (Pratt, 1974). *Crepidula fornicata* was the only species in this study that was present at every locality in both study areas, that colonized substrates by stacking, and that released planktotrophic larvae. Stacking and pelagic larval distribution contributed to *C. fornicata*'s occurrence at each locality because possessing such traits enabled *C. fornicata* to tolerate and adapt to temporal and spatial variations in the environment.

Objectives

The purpose of this study is to determine if predator-prey interaction plays a significant role in evolution, and how a predator-prey system varies between two separate environments. This study compares various predation indices between drilling muricid and naticid gastropods and a single prey genus through time for both a temperate and sub-tropical environment. Gastropod prey belonging to the genus *Crepidula* were used for this study. *Crepidula* were selected because they are common prey for both naticid and muricid gastropods, they have a broad geographic and geologic range, and they are abundant in the fossil record. Most *Crepidula* species have remained extant since the Miocene, and, although evolutionary change in the form of speciation is rare, many *Crepidula* species have undergone directional morphologic change through time in response to local changes in biotic and abiotic conditions of the environments they inhabit. Environmental change has resulted in species variability through time, as well as between populations living in separate environments at the same time (Hoagland, 1977).

Many studies addressing the role that predator-prey interaction plays in evolution, particularly those supporting escalation, use faunal assemblages from various formations, and have shown that escalation at the faunal level is triggered by changes in the physical environment that are often caused by episodes of mass extinction (Kelley and Hansen, 1996; Hansen et al., 1999; Vermeij, 1994). Mass extinctions disrupt faunal structure by eliminating certain taxonomic groups allowing their niche space to be filled with new or immigrant taxa, which then reconfigures ecosystems by eliminating key members of the food chain (Kelley and Hansen, 1996). However, evolutionary change within a lineage depends on the adaptive capabilities of a species in response to changes in the environment as well as competition and predation (Kelley and Hansen, 2001; Vermeij, 1987). Therefore, escalation and/or coevolution at the lineage level may be the result of an increase or decrease in predation and/or competition, and is not necessarily influenced by environmental changes associated with mass extinctions. Narrowing a study to a single prey genus that is geographically widespread, is abundant in the fossil record, and has survived a mass extinction event would help to better understand the role of both ecologic interaction and mass extinctions in evolution. This type of study enables one to interpret morphologic changes within a lineage that were brought on by predator-prey interaction in separate environments, and also can determine if such changes enhanced survivorship from a mass extinction event.

I analyzed *Crepidula* populations from various formations in Florida, South Carolina, North Carolina, and Virginia that range from middle Pliocene to Pleistocene in age and determined variations in species relative abundances, size distributions, and predation indices between populations. Molluscan faunas from Florida contain more sub-tropical taxa than those from South Carolina, North Carolina, and Virginia, and many molluscan groups were restricted to one of the two geographic areas. Five *Crepidula* species were examined in this study, and four of those species occurred in both areas, allowing predator-prey interaction of this particular system to be evaluated through time in two separate environments. The following species were examined: *Crepidula aculeata*, *C. convexa*, *C. plana*, *C. maculosa* (restricted to Florida), and *C. fornicata* (Figure 3a-e). All five species are extant and all originated before the oldest formation in this study was deposited.

Samples from Florida contain both Atlantic and Gulf Coastal Plain formations, which were analyzed separately for temporal variations, and Atlantic and Gulf Coastal Plain formations were compared for spatial variations. *Crepidula* from South Carolina, North Carolina, and Virginia formations were placed in stratigraphic order to determine temporal trends in drilling predation, and data from several correlative formations were compared for spatial variations. Data collected from Florida formations were also compared to those from correlative formations in North Carolina, and Virginia in order to determine spatial variations between *Crepidula* populations in separate environments with respect to species diversity and size, as well as predation indices.

There are several objectives to this study.

1. To compare predation data among four Plio-Pleistocene localities in Florida (two Gulf Coastal

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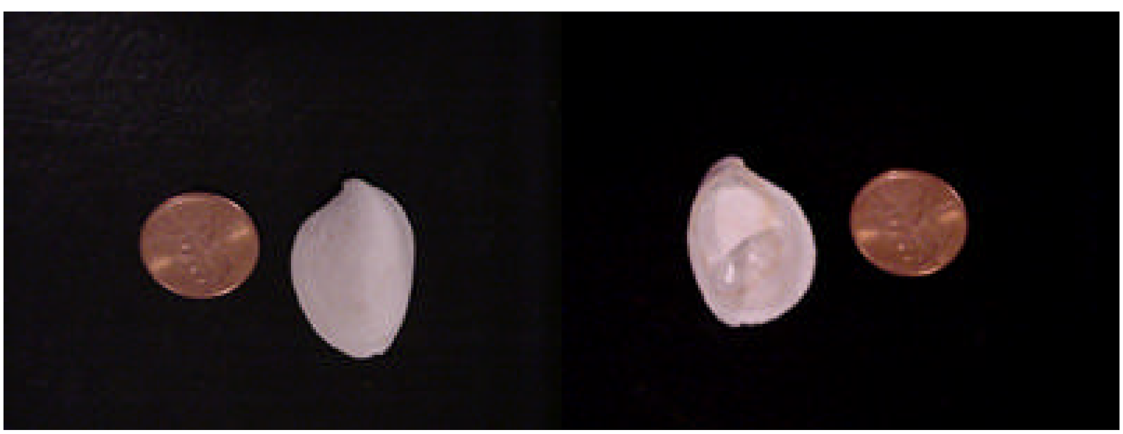
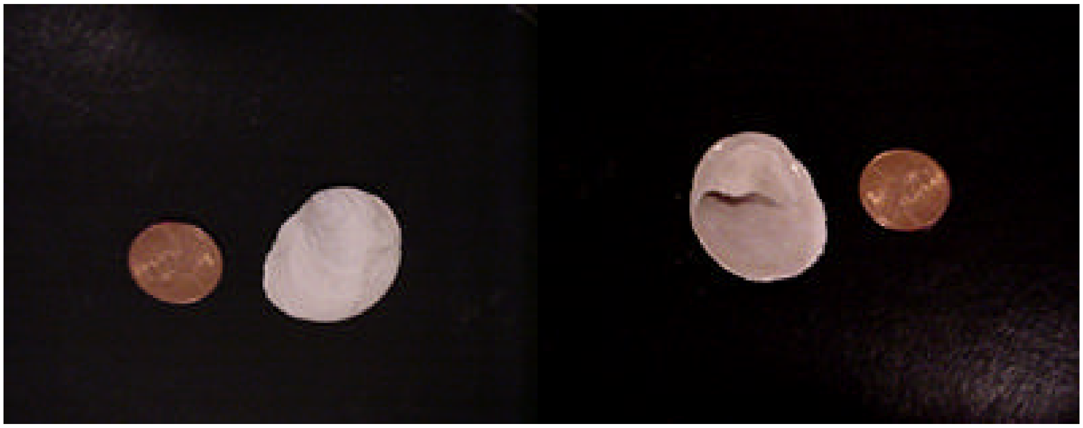
c. 

d. 

e. 

Figure 3a., b., c., d., e.) a.) Specimen of *Crepidula aculeata* from dorsal (left) and ventral (right) view. b.) Specimen of *C. convexa* from dorsal (left) and ventral (right) view. c.) Specimen of *C. maculosa* from dorsal (left) and ventral (right) view. d.) Specimen of *C. plana* from dorsal (left) and ventral (right) view. e.) Specimen of *C. fornicata* from dorsal (left) and ventral (right) view.

localities and two Atlantic Coastal localities), determining temporal and/or spatial variations of this particular predator-prey system.

2. To compare predation data among eight Plio-Pleistocene formations in South Carolina, North Carolina, and Virginia, determining temporal trends of this predator-prey system.

3. To determine if this particular predator-prey system provides evidence for escalation, and/or provides evidence of coevolution.

4. To also compare predation data from formations in Florida to those from their general correlative counterparts in South Carolina, North Carolina, and Virginia and determine any significant differences and possible implications of these differences.

5. Lastly, to see if Pliocene *Crepidula* populations differ from Pleistocene *Crepidula* populations with regards to species relative abundances and size distributions, and predation indices for both study areas in order to determine if the Plio-Pleistocene mass extinction affected the tempo and mode of evolution within the genus *Crepidula*.

## MATERIALS AND METHODS

### Study Area

Plio-Pleistocene shallow-water marine deposits along the US Atlantic and Gulf Coastal Plain contain an abundance of well-preserved molluscan fossils. Fossil assemblages within these deposits make up three subprovinces of the large Plio-Pleistocene molluscan faunal province, the Caloosahatchian (Petuch, 1988). Plio-Pleistocene formations along the US Atlantic Coastal Plain, excluding Florida, contain molluscan faunas in the Yorktownian subprovince (Figure 4(1)). Molluscan faunas along the Atlantic and Gulf Coastal Plain of the Florida peninsula make up the Buckinghamian subprovince (Figure 4(2)). The Jacksonbluffian molluscan subprovince includes faunas along the US Gulf Coastal Plain of the Florida panhandle and extends westward to the southern tip of Texas (Figure 4(3)). Faunal assemblages used in this study were collected from Plio-Pleistocene formations in the Yorktownian and Buckinghamian molluscan subprovinces. In general, Buckinghamian faunas in Florida contained more tropical species of molluscs than the Yorktownian faunas to the north (Randazzo and Jones, 1997).

Yorktownian Subprovince

Plio-Pleistocene Yorktownian faunas were collected from eight Atlantic Coastal Plain localities (Figure 5). These localities are environmentally similar, consisting of marine inner shelf clastic deposits. Several episodes of global warming and cooling caused a series of transgressive and regressive cycles in the late Pliocene and early Pleistocene that left extensive clastic marine deposits along the US Atlantic Coastal Plain in Virginia, North Carolina, and South Carolina (Blackwelder, 1981). These deposits have been assigned to a number of formations that are lithologically distinct and recognized as separate stratigraphic units (Blackwelder, 1981). Pliocene localities included the Rushmere Member (Mbr.) of the Yorktown Formation (Fm.), Lt. Run, Virginia; the Moore House Mbr. of the Yorktown Fm., Chuckatuck, Virginia; the Chowan River Fm., Gomez Pit, Virginia; the Duplin Fm., Lumberton, North Carolina; and the Raysor Fm., near Goose Creek, South Carolina. Pleistocene localities included the first phase of the Waccamaw Fm., Old Dock, North Carolina; the second phase of the Waccamaw Fm., Shallotte, North Carolina; and the James City Fm., Aurora, North Carolina. According to Herbert and Portell (pers. comm.), the first phase of the Waccamaw Fm. may include both late Pliocene and early Pleistocene deposits based on the occurrence of several taxa that went extinct at the end of the Pliocene in Florida. Therefore, it was considered as a Plio-Pleistocene locality in this study and placed stratigraphically between the Chowan River Fm. and the James City Formation.

All of the Yorktownian formations used in this study represent transgressive and highstand deposits that accumulated during periods of warming in the late Pliocene and early Pleistocene (Zullo and Harris, 1992). Global warming and ice melting caused extensive flooding and sediment accumulation on the Coastal Plain. Large portions of these deposits were preserved and make up the various Plio-Pleistocene Coastal Plain formations that are recognized today. The lithology of each formation varies slightly and generally consists mostly of fossiliferous sand

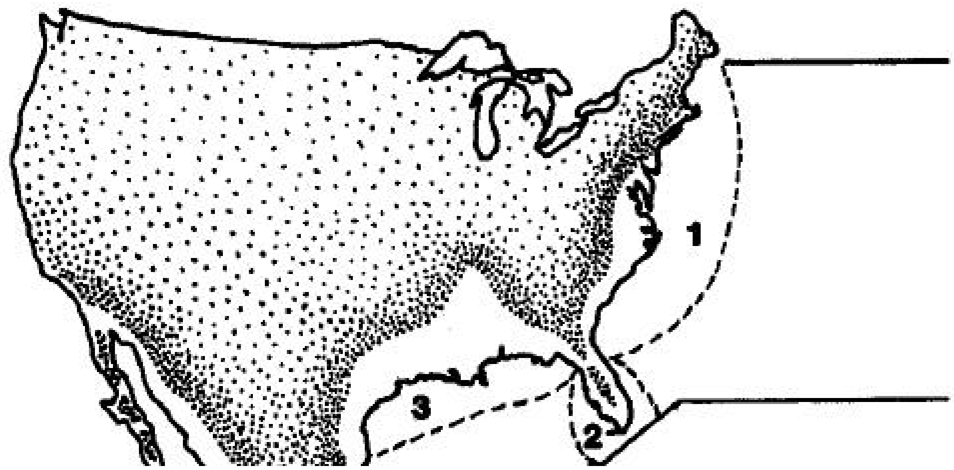



Figure 4. Three subprovinces of the Plio-Pleistocene shallow-water marine molluscan province, the Caloosahatchian. 1: Yorktownian; 2: Buckinghamian; 3: Jacksonbluffian (after Petuch, 1988).


Figure 5. Location of the eight Yorktownian localities sampled in this study. Pliocene localities, indicated by yellow dots, included: A, Raysor Formation; B, Duplin Formation; C, Rushmere Member of the Yorktown Formation; D, Moore House Member of the Yorktown Formation; and E, Chowan River Formation. Pleistocene localities, indicated by red dots, included: F, 1st phase of the Waccamaw Formation; G, 2nd phase of the Waccamaw Formation; and H, James City Formation.

mixed with other marine clastic sediments (Zullo and Harris, 1992). The depositional environments of these formations are similar, and the faunas collected from these formations represent within habitat time averaged assemblages (Hansen and Kelley, 1995). Therefore, time averaging may decrease the temporal resolution of predation patterns in this study, but variations in drilling predation that are caused by differences in the physical environment should not be a factor. There have been few, if any, detailed studies on the taphonomy of sampled units; however, previous studies on naticid predation from these units suggest that taphonomic bias was minimized (Hansen and Kelley, 1993, 1995, 1996). In general, *Crepidula* specimens from these units displayed no evidence of taphonomic alteration, such as dissolution or fragmentation. There may be a preservational bias of specimens within a certain size range due to winnowing and/or sorting of material, but these should be minimized because methods used to collect samples were kept consistent.

Buckinghamian Subprovince

Plio-Pleistocene Buckinghamian faunas were collected from two Atlantic Coastal Plain localities and two Gulf Coastal Plain localities (Figure 6). Atlantic Coastal Plain localities included the Nashua Fm. (uppermost Pliocene), Cracker Swamp, Florida, and the Bermont Fm. (lower Pleistocene), near West Palm Beach, Florida. Gulf Coastal Plain localities included bed 3 of the upper Pinecrest beds of the Tamiami Fm. (upper Pliocene), near Sarasota, Florida, and the Bermont Fm. (lower Pleistocene), near Naples, Florida. Most of the upper Pinecrest beds represent highstand deposits, and bed 3 is characterized by densely packed fossils of shallow marine molluscs in a matrix of clean quartz sand (Zullo and Harris, 1992). The Bermont Fm. is composed of siliciclastic to mixed siliciclastic-carbonate sands and contains an abundance of well-preserved, diverse molluscan fossils (Zullo and Harris, 1992). The Bermont Fm. was recognized by DuBar (1971) as a distinct biostratigraphic unit between the Caloosahatchee and Fort Thompson formations. The Bermont Fm. is lithologically similar to the underlying Caloosahatchee Fm., but can be distinguished based on faunal differences (Zullo and Harris,

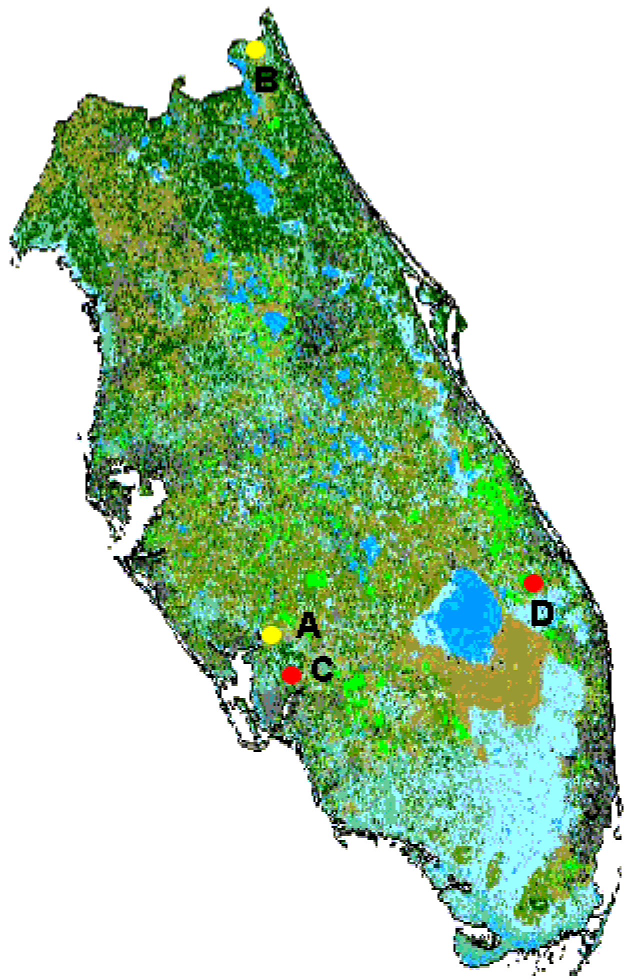



Figure 6. Location of the four Buckinghamian localities sampled in this study. Pliocene localities, indicated by the yellow dots, included: A, Pinecrest Beds (bed 3) of the Tamiami Formation; and B, Nashua Formation. Pleistocene localities, indicated by the red dots, included: C, Bermont Formation (Gulf Coast); and D, Bermont Formation (Atlantic Coast).

1992). The Nashua Fm. is a quartz-dominant sand that alternates between a medium-grain, variably calcareous, shelly sand to finely sandy coquina (Huddlestun, 1988). The Nashua Fm. is a lithologically distinct, mappable formation placed stratigraphically between the underlying Coosawhatchie Fm. and overlying Cypresshead Formation (Huddlestun, 1988; Scott, 1992).

Studies addressing the taphonomy of these sampled units are also very generalized (Allmon, 1992). The formations are environmentally similar and the assemblages within these deposits represent within habitat time averaged, and therefore variations in drilling predation that are caused by environmental differences should not be a factor. Fossil preservation in these formations is excellent, and *Crepidula* specimens do not appear to have been taphonomically altered.

Sampling Techniques

Fieldwork was conducted on various dates between the fall of 2000 and fall of 2001. Mollusc assemblages were bulk sampled from the Moore House Mbr. of the Yorktown Fm. (Pliocene), Chuckatuck, Virginia; the first phase of the Waccamaw Fm. (Plio-Pleistocene), Old Dock, North Carolina; the second phase of the Waccamaw Fm. (Pleistocene), Shallotte, North Carolina; the James City Fm. (Pleistocene), Aurora, North Carolina; and two localities of the Bermont Fm. (Pleistocene), near West Palm Beach and Naples, Florida. Bulk samples from each locality were wet sieved using a sieve 3mm in size, and all complete *Crepidula* specimens (>3mm) were picked from each sample. *Crepidula* specimens were also hand picked in the field at each locality. Hand picking was conducted by carefully surveying an area that measured approximately 3 feet by 3 feet and collecting all *Crepidula* specimens within the plotted area.

*Crepidula* specimens used in this study were also obtained through collections at the Florida Museum of Natural History, Gainesville, FL, and the Virginia Museum of Natural History, Martinsville, VA. All *Crepidula* from these museum collections also came from bulk sampled mollusc assemblages. Museum specimens were collected from the Raysor Fm. (Pliocene), near Goose Creek, South Carolina; the Duplin Fm. (Pliocene), Lumberton, North Carolina; the

Rushmere Mbr. of the Yorktown Fm. (Pliocene), at Gomez Pit, Virginia; the Nashua Fm. (Plio-Pleistocene), Cracker Swamp, Florida; and the Pinecrest Beds (#3) of the Tamiami Fm. (Pliocene), near Sarasota, Florida. *Crepidula* specimens collected in the field and those obtained through museum collections were identified to the species level.

Predation Indices

Drilled mollusc specimens collected from fossil assemblages provide information not only about the prey but also about the predator's taxonomic affinity, size, borehole site selectivity, and whether or not the attack was successful (Kelley and Hansen, 1996). Therefore, naticid and muricid predator-prey interaction can be reconstructed using drilled specimens from fossil assemblages of molluscan faunas. Data on naticid and muricid predation are commonly used in studies that try to determine the role that ecological interactions plays in evolution, and in particular, studies testing escalation and coevolution.

*Crepidula* specimens collected from each locality were examined for the presence of naticid and muricid drillholes, and drilled specimens were used to tabulate data on naticid and muricid predation. Prey specimens with complete and incomplete drillholes were used to help interpret predator-prey interactions. Naticid and muricid predation indices were calculated separately and combined for all *Crepidula* species at each locality, and also for the entire genus from each locality. The following indices were determined: predation intensity, prey effectiveness, drillhole-site selectivity, prey species selectivity, and prey size selectivity.

Predation Intensity

Compilations of gastropod drilling frequencies have been used frequently in studies testing escalation and coevolution (Vermeij, 1987; Kelley and Hansen, 1996b). Predation intensity is determined by calculating muricid and naticid drilling frequencies, which measures the percentage of individuals in a fauna that were successfully drilled by these predatory gastropods. Drilling frequencies were calculated by dividing the number of individuals with one or more complete drillholes by the total number of *Crepidula* specimens in the sample. Naticid and muricid drilling frequencies were calculated separately and combined for every *Crepidula* species at each locality, as well as for the entire genus from each locality. Drilling frequencies from successive formations and time correlative formations were compared statistically to determine temporal and spatial variations in naticid and muricid predation intensity.

Prey Effectiveness

Incomplete drillholes are also used to study escalation and coevolution because they represent unsuccessful attacks by the predator possibly due to adaptations of the prey. Prey effectiveness measures the percent of drillholes that are incomplete, and is determined by dividing the number of incomplete drillholes in a sample by the total number of attempted drillholes (Vermeij, 1987). The frequency of incomplete muricid and the combined total of naticid and muricid drillholes were calculated for all *Crepidula* species and the entire genus from each locality. Naticid prey effectiveness values were not calculated separately because incomplete naticid drillholes were rare or absent in most samples. Prey effectiveness values from successive and time-correlative formations were also compared statistically to show temporal and spatial variations in the effectiveness of the prey.

Drillhole-site Selectivity

Studies have shown that naticids and muricids exhibit selectivity with respect to drillhole site on the prey shell in order to maximize net energy gain (Kitchell et al., 1981; Kelley and Hansen, 1996; Dietl and Alexander, 2000; Dietl, 2000; Hughes and Dunkin, 1984). Stereotyped behavior of naticids and muricids has developed over geologic time, providing further evidence for escalation and coevolution (Kitchell et al., 1981).

*Crepidula* specimens with complete naticid and muricid drillholes were surveyed and the location of each drillhole was recorded with respect to a five-sector grid superimposed on the prey shell (Figure 7). The five-sector grid was placed on a sheet of graph paper (10 x 10 to the cm) in order to determine the percent area that each sector covered. The surface area of each sector was determined by dividing the number of squares per sector by the total number of

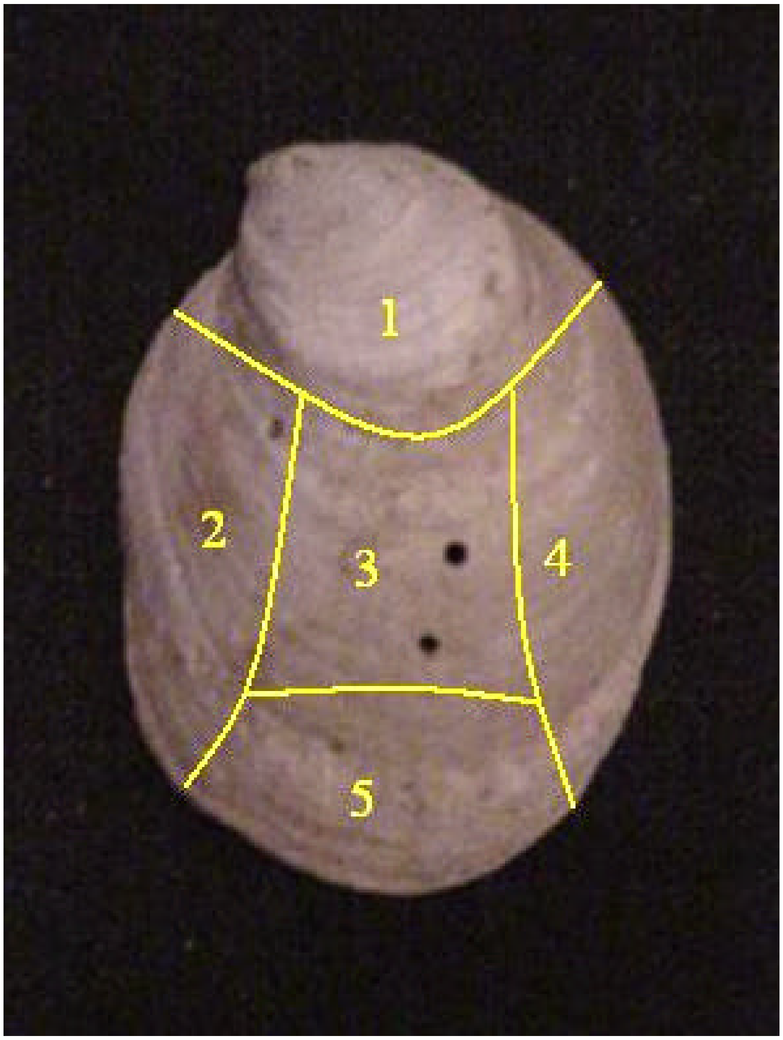



Figure 7. Diagram of a five-sector grid superimposed on a *Crepidula* specimen that was used to determine drillhole-site selectivity.

squares for the entire grid. A chi-squared test was conducted to determine whether drilling was site selective for each prey species. Chi-squared tests determined if the number of drillholes in a sector was proportional to that sector's area. Chi-squared values larger than 5.99 indicated drilling was non-random. Naticid and muricid drillhole site selectivity on *C. fornicata* and the entire genus was determined for Pliocene samples and Pleistocene samples from Yorktownian and Buckinghamian localities.

Prey Species Selectivity

Studies have shown that naticids and muricids exhibit selectivity with respect to prey species in order to maximize net energy gain (Kitchell et al., 1981; Kelley and Hansen, 1996; Dietl and Alexander, 2000; Dietl, 2000; Alexander and Dietl, 2001; Hughes and Dunkin, 1984). Naticid and muricid predation may be influenced by the abundance of certain prey species in a fauna. Therefore, relative abundances of prey species can aid the interpretation of predation indices within a particular fauna, and also help in interpreting temporal and spatial variations in prey effectiveness and predation intensity from different faunas.

The relative abundances of all *Crepidula* species with respect to the entire genus collected from each locality were determined by dividing the number of individuals per species by the total number of individuals in the entire population. Individuals were surveyed for the presence of muricid and/or naticid drillholes, and the number of individuals with one or more complete drillhole was recorded. Ratios of drilled to undrilled specimens for each species were compared statistically to one another using a Fisher's exact test in order to determine if muricids and/or naticids were selective with respect to species. A Fisher's exact test was used because it takes into account marginal differences with respect to the number of specimens in a species.

Prey Size Selectivity

Studies have also shown that naticids and muricids exhibit selectivity with respect to prey size in order to maximize net energy gain (Kitchell et al., 1981; Kelley and Hansen, 1996; Dietl and Alexander, 2000; Dietl, 2000; Hughes and Dunkin, 1984). Shell length of all *Crepidula* specimens from each locality was measured to the nearest 0.1mm with a digital caliper and used to determine specimen size. *Crepidula* sizes were used to generate size frequency histograms using 10mm increments for each species and the entire *Crepidula* genus from a locality. Size frequency histograms also displayed the number of drilled specimens within each size class. Two histograms were generated, one showing the number of specimens drilled by muricids within each size class, and the other showing the number of specimens drilled by naticids within each size class. The percentages of drilled specimens from each size class were compared statistically using a Fisher's exact test in order to determine if muricids and naticids were selective with respect to prey size for that particular locality.

## RESULTS

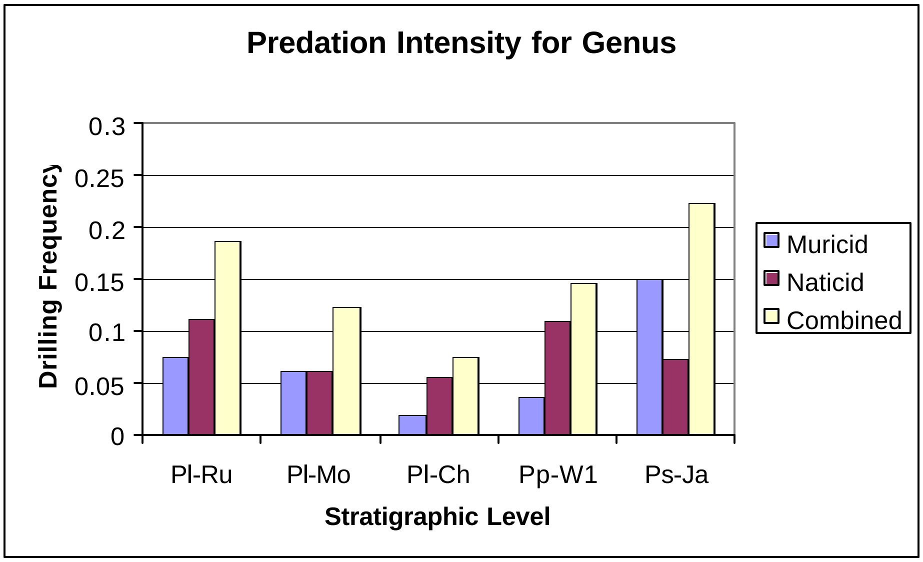
### Predation Intensity

#### Yorktownian Localities

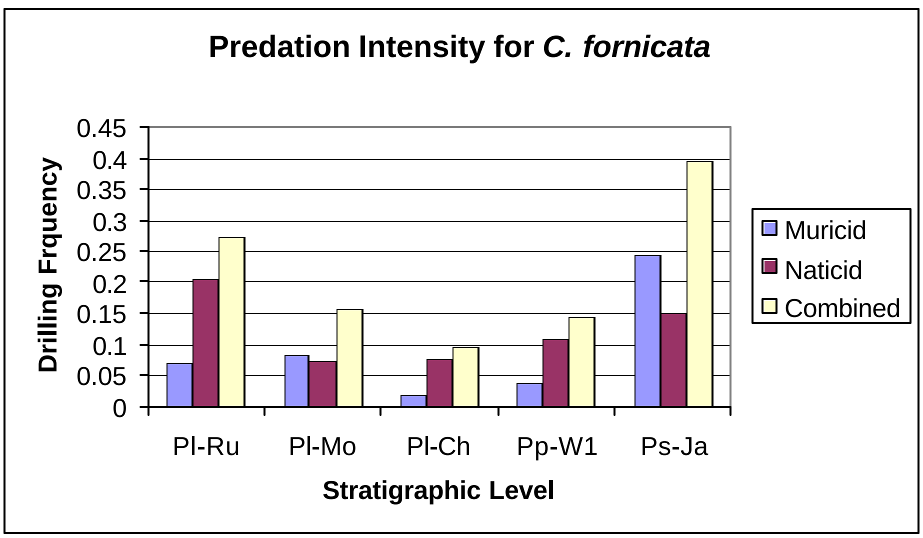
Muricid (MDF), naticid (NDF), and combined (CDF) drilling frequencies on individual *Crepidula* species and the entire genus were calculated for each Yorktownian locality to determine predation intensity along the Atlantic Coastal Plain throughout the Plio-Pleistocene (Table 1). Muricid and naticid drilling on the genus *Crepidula* was moderate in the middle Pliocene (7.5% and 11.2% respectively), steadily decreased through the late Pliocene (1.9% and5.6%), and then increased to moderately high levels in the Pleistocene (15.0% and 7.2%, Figure 8a). The Rushmere Mbr. of the Yorktown Fm. is closer geographically to the Moore House Mbr. of the Yorktown Fm. than both the correlative Raysor and Duplin formations. Therefore, Middle Pliocene drilling frequencies used for temporal comparisons were obtained from the Rushmere Mbr. of the Yorktown Fm. because they are less likely to be influenced by differences in the environment. Drilling frequencies were compared using a chi-squared test, and it was determined that muricid drilling frequencies from the first phase of the Waccamaw Fm. were significantly lower than in the James City Fm. ($p = 0.0008$, Table 2). Comparisons showed

| Locality (age) | Species | MDF | NDF | CDF |
|---|---|---|---|---|
| James City (E-Pleist) | *C. fornicata* | 0.245 | 0.151 | 0.396 |
| | *C. aculeata* | 0.108 | 0.042 | 0.15 |
| | Genus | 0.15 | 0.072 | 0.222 |
| 2nd Waccamaw (E-Pleist) | *C. fornicata* | 0.091 | 0.052 | 0.143 |
| | Genus | 0.089 | 0.063 | 0.152 |
| 1st Waccamaw (Plio-Pleist) | *C. fornicata* | 0.036 | 0.109 | 0.145 |
| | Genus | 0.036 | 0.109 | 0.145 |
| Chowan River (L-Plio) | *C. fornicata* | 0.019 | 0.077 | 0.096 |
| | *C. plana* | 0.026 | 0.026 | 0.051 |
| | Genus | 0.019 | 0.056 | 0.075 |
| Moore House (ML-Plio) | *C. fornicata* | 0.082 | 0.074 | 0.156 |
| | *C. aculeata* | 0.029 | 0.043 | 0.073 |
| | Genus | 0.061 | 0.061 | 0.122 |
| Rushmere (M-Plio) | *C. fornicata* | 0.068 | 0.205 | 0.273 |
| | *C. aculeata* | 0.082 | 0.049 | 0.131 |
| | Genus | 0.075 | 0.112 | 0.187 |
| Duplin (M-Plio) | *C. fornicata* | 0.11 | 0.03 | 0.136 |
| | *C. plana* | 0 | 0.043 | 0.043 |
| | Genus | 0.079 | 0.03 | 0.109 |
| Raysor (M-Plio) | *C. fornicata* | 0.044 | 0.082 | 0.133 |
| | *C. convexa* | 0.083 | 0 | 0.083 |
| | *C. aculeata* | 0.045 | 0.182 | 0.227 |
| | Genus | 0.053 | 0.085 | 0.138 |

Table 1. Compilation of muricid (MDF), naticid (NDF), and combined (CDF) drilling frequencies for all *Crepidula* species (>20 specimens) at each Yorktownian locality. Middle Pliocene (M-Plio) localities included the Raysor Formation of South Carolina, the Duplin Formation of North Carolina, and the Rushmere Member of the Yorktown Formation of Virginia. Middle-late Pliocene (ML-Plio) localities included the Moore House Member of the Yorktown Formation of Virginia. Late Pliocene (L-Plio) localities included the Chowan River Formation of Virginia. Plio-Pleistocene (Plio-Pleist) localities included the first phase of the Waccamaw Formation of North Carolina. Early Pleistocene (E-Pleist) localities included the second phase of the Waccamaw Formation and the James City Formation of North Carolina.




a.




b.

Figure 8. a., b.) Drilling frequencies through time for the genus *Crepidula* (a.) and the species *C. fornicata* (b.) from selected Pliocene and Pleistocene localities of the Yorktownian molluscan subprovince. Abbreviations for stratigraphic levels are as follows. Pliocene levels (designated Pl): Ru, Rushmere Member of the Yorktown Formation of Virginia; Mo, Moore House Member of the Yorktown Formation of Virginia; Ch, Chowan River Formation. Plio-Pleistocene levels (designated Pp): W1, 1st phase of the Waccamaw Formation of North Carolina. Pleistocene levels (designated Ps): Ja, James City Formation of North Carolina.

| Formations | Drilled Specimens | | | Undrilled Specimens | | | Chi^2 probabilities | | |
|---|---|---|---|---|---|---|---|---|---|
| | M | N | C | M | N | C | M | N | C |
| James City | 27 | 13 | 40 | 153 | 167 | 140 | | | |
| 1st Waccamaw | 5 | 15 | 20 | 133 | 123 | 118 | 0.0008* | 0.255 | 0.081 |
| | | | | | | | | | |
| 1st Waccamaw | 5 | 15 | 20 | 133 | 123 | 118 | | | |
| Chowan River | 2 | 6 | 8 | 105 | 101 | 99 | 0.414 | 0.144 | 0.087 |
| | | | | | | | | | |
| Chowan River | 2 | 6 | 8 | 105 | 101 | 99 | | | |
| Moore House | 12 | 12 | 24 | 185 | 185 | 173 | 0.093 | 0.864 | 0.202 |
| | | | | | | | | | |
| Moore House | 12 | 12 | 24 | 185 | 185 | 173 | | | |
| Rushmere | 8 | 12 | 20 | 99 | 95 | 87 | 0.642 | 0.114 | 0.123 |

Table 2. Chi-squared comparison of muricid (M), naticid (N), and combined (C) drilling frequencies on the genus *Crepidula* between stratigraphic successive formations of the Yorktownian subprovince. Statistically significant differences ($p < 0.05$) are indicated with a (*).

no significant temporal variations in naticid or combined drilling frequencies between successive formations.

Muricid, naticid, and combined drilling frequencies on the species *Crepidula fornicata* showed a trend similar to that seen for the entire genus (Figure 8b). Drilling frequencies on *C. fornicata* were also compared using a chi-squared test (Table 3). Naticid drilling significantly decreased from the Rushmere Mbr. (20.5%) to the Moore House Mbr. (7.4%) of the Yorktown Formation (p = 0.016, Table 3). Muricid and combined drilling frequencies from the first phase of the Waccamaw Fm. (3.6% and 14.5% respectively) to the James City Fm. (24.5% and 39.6%) showed a significant increase (p = 0.0001 and p = 0.001, Table 3).

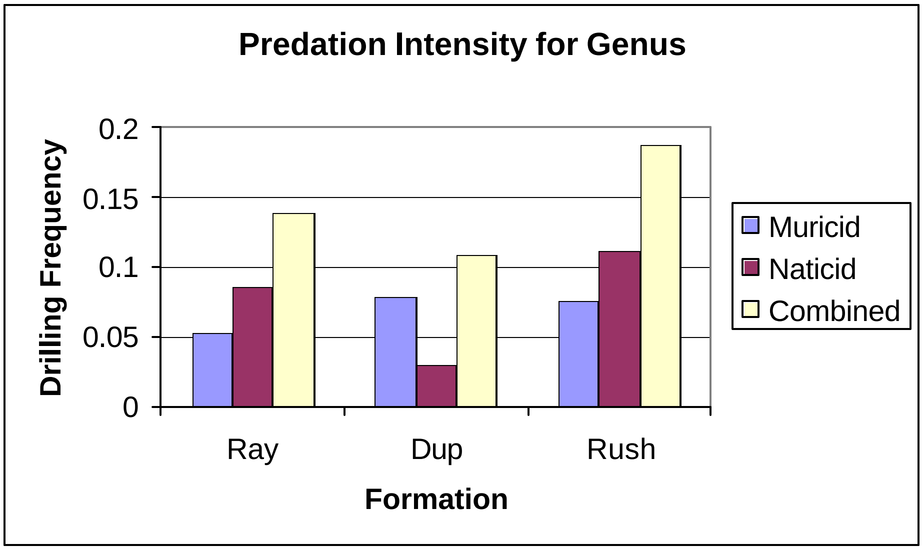
Muricid, naticid, and combined drilling frequencies for the Raysor Fm., the Duplin Fm., and the Rushmere Mbr. of the Yorktown Fm. were also compared to determine spatial variations in predation intensity. Muricid and combined drilling frequencies on *C. fornicata* and the genus showed some variation between these correlative formations, but chi-squared comparisons indicated that changes were not significant (Figure 9a and b, Tables 4 and 5). Chi-squared comparisons of naticid drilling frequencies from the Duplin Fm. and the Rushmere Mbr. of the Yorktown Fm. on *C. fornicata* (3.0% and 20.5% respectively) and the genus (3.0% and 11.2%) did, however, show a significant difference (p = 0.003, Table 5, and p = 0.023, Table 4).

Buckinghamian Localities

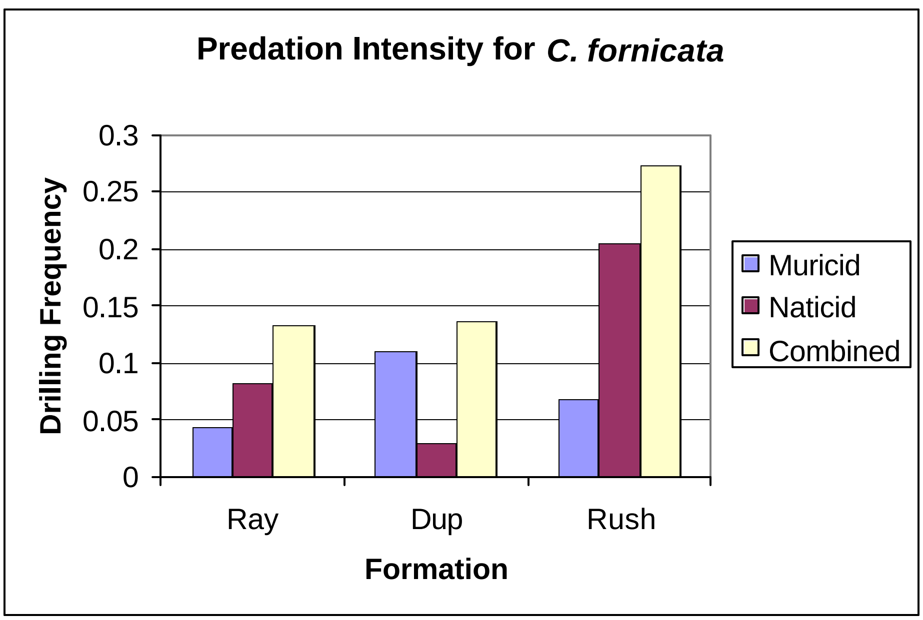
Muricid (MDF), naticid (NDF), and combined (CDF) drilling frequencies on *Crepidula* species and the entire genus from four Buckinghamian localities (3 stratigraphic levels) were calculated to determine fluctuations in predation intensity along the Atlantic and Gulf Coastal Plain in Florida during the Plio-Pleistocene (Table 6). Muricid, naticid, and combined drilling frequencies on the genus were extremely low in the late Pliocene (1.7%, 0%, and 1.7% respectively), and then increased at the Plio-Pleistocene boundary (7.7%, 1%, and 8.7%), and naticid drilling continued to increase (4%), while muricid and combined drilling frequencies decreased into the Pleistocene (2.4% and 6.4% respectively, Figure 10). Drilling frequencies for

| Formations | Drilled Specimens | | | Undrilled Specimens | | | Chi^2 probabilities | | |
|---|---|---|---|---|---|---|---|---|---|
| | M | N | C | M | N | C | M | N | C |
| James City | 13 | 8 | 21 | 40 | 45 | 32 | | | |
| 1st Waccamaw | 5 | 15 | 20 | 133 | 123 | 118 | 0.0001* | 0.421 | 0.001* |
| 1st Waccamaw | 5 | 15 | 20 | 133 | 123 | 118 | | | |
| Chowan River | 1 | 4 | 5 | 51 | 48 | 47 | 0.55 | 0.515 | 0.375 |
| Chowan River | 1 | 4 | 5 | 51 | 48 | 47 | | | |
| Moore House | 10 | 9 | 19 | 112 | 113 | 103 | 0.119 | 0.942 | 0.296 |
| Moore House | 10 | 9 | 19 | 112 | 113 | 103 | | | |
| Rushmere | 3 | 9 | 12 | 41 | 35 | 32 | 0.085 | 0.016* | 0.087 |

Table 3. Chi-squared comparison of muricid (M), naticid (N), and combined (C) drilling frequencies on the species *C. fornicata* between stratigraphic successive formations of the Yorktownian subprovince. Statistically significant differences ($p < 0.05$) are indicated with a (*).




a.




b.

Figure 9. a., b.) Drilling frequencies for the genus *Crepidula* (a.) and the species *C. fornicata* (b.) from 3 correlative Pliocene localities of the Yorktownian subprovince. Localities include the Raysor (Ray) Formation of South Carolina, the Duplin (Dup) Formation of North Carolina, and the Rushmere (Rush) Member of the Yorktown Formation of Virginia.

| Formations | Drilled Specimens | | | Undrilled Specimens | | | Chi^2 probabilities | | |
|---|---|---|---|---|---|---|---|---|---|
| | M | N | C | M | N | C | M | N | C |
| Raysor | 5 | 8 | 13 | 89 | 86 | 81 | 0.464 | 0.094 | 0.533 |
| Duplin | 8 | 3 | 11 | 93 | 98 | 90 | | | |
| | | | | | | | | | |
| Raysor | 5 | 8 | 13 | 89 | 86 | 81 | 0.535 | 0.523 | 0.353 |
| Rushmere | 8 | 12 | 20 | 99 | 95 | 87 | | | |
| | | | | | | | | | |
| Duplin | 8 | 3 | 11 | 93 | 98 | 90 | 0.904 | 0.023* | 0.114 |
| Rushmere | 8 | 12 | 20 | 99 | 95 | 87 | | | |

Table 4. Chi-squared comparison of muricid (M), naticid (N), and combined (C) drilling frequencies on the genus *Crepidula* between correlative Pliocene formations of the Yorktownian subprovince. Statistically significant differences ($p < 0.05$) are indicated with a (*).

| Formations | Drilled Specimens | | | Undrilled Specimens | | | Chi^2 probabilities | | |
|---|---|---|---|---|---|---|---|---|---|
| | M | N | C | M | N | C | M | N | C |
| Raysor | 2 | 4 | 6 | 43 | 41 | 39 | 0.243 | 0.18 | 0.963 |
| Duplin | 7 | 2 | 9 | 59 | 64 | 57 | | | |
| Raysor | 2 | 4 | 6 | 43 | 41 | 39 | 0.627 | 0.122 | 0.102 |
| Rushmere | 3 | 9 | 12 | 41 | 35 | 32 | | | |
| Duplin | 7 | 2 | 9 | 59 | 64 | 57 | 0.498 | 0.003* | 0.075 |
| Rushmere | 3 | 9 | 12 | 41 | 35 | 32 | | | |

Table 5. Chi-squared comparison of muricid (M), naticid (N), and combined (C) drilling frequencies on the species *C. fornicata* between correlative Pliocene formations of the Yorktownian subprovince. Statistically significant differences ($p < 0.05$) are indicated with a (*).

| **Locality (age)** | **Species** | **MDF** | **NDF** | **CDF** |
|---|---|---|---|---|
| Gulf Coast Bermont (Pleist) | *C. fornicata* | 0.091 | 0.182 | 0.273 |
| | *C. aculeata* | 0 | 0.023 | 0.023 |
| | Genus | 0.011 | 0.033 | 0.044 |
| | | | | |
| Atl. Coast Bermont (Pleist) | *C. fornicata* | 0.167 | 0 | 0.167 |
| | *C. maculosa* | 0.018 | 0.055 | 0.073 |
| | *C. convexa* | 0 | 0.037 | 0.037 |
| | *C. aculeata* | 0.051 | 0.051 | 0.102 |
| | Genus | 0.029 | 0.044 | 0.072 |
| | | | | |
| Combined Bermont (Pleist) | *C. fornicata* | 0.13 | 0.087 | 0.217 |
| | *C. maculosa* | 0.013 | 0.04 | 0.053 |
| | *C. convexa* | 0 | 0.031 | 0.031 |
| | *C. aculeata* | 0.029 | 0.039 | 0.069 |
| | Genus | 0.024 | 0.04 | 0.064 |
| | | | | |
| Nashua (Plio-Pleist) | *C. fornicata* | 0.087 | 0.007 | 0.094 |
| | *C. plana* | 0.046 | 0 | 0.046 |
| | *C. convexa* | 0.063 | 0.021 | 0.083 |
| | Genus | 0.077 | 0.01 | 0.087 |
| | | | | |
| Pinecrest Bed 3 (L-Plio) | *C. fornicata* | 0.019 | 0 | 0.019 |
| | Genus | 0.017 | 0 | 0.017 |

Table 6. Compilation of muricid (MDF), naticid (NDF), and combined (CDF) drilling frequencies for all *Crepidula* species (>20 specimens) at each Buckinghamian locality.

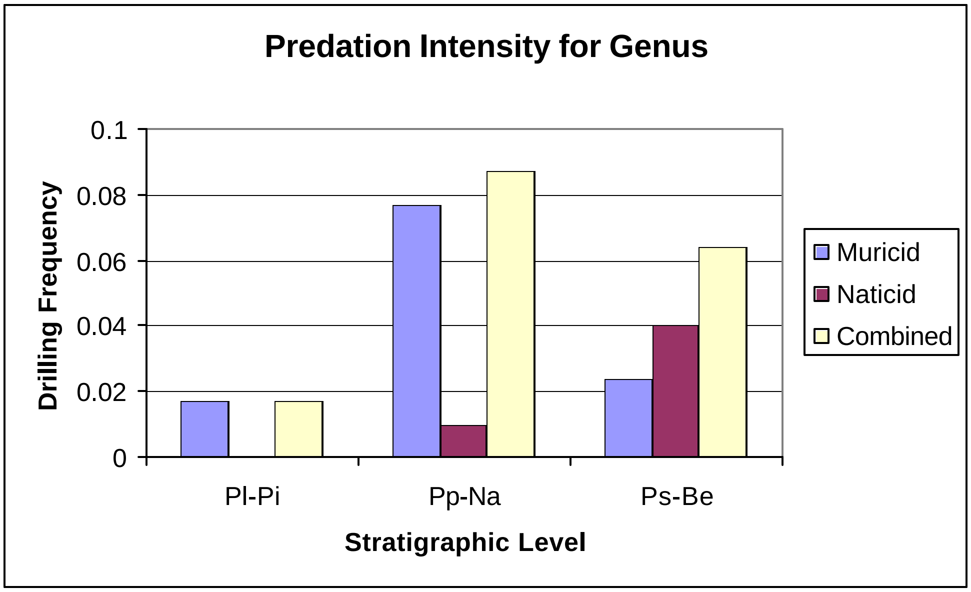



Figure 10. Drilling frequencies through time for the genus *Crepidula* from Pliocene and Pleistocene localities of the Buckinghamian molluscan subprovince. Abbreviations for stratigraphic levels are as follows. Pliocene levels (designated Pl): Pi, Pinecrest Beds (bed 3) of the Tamiami Formation of Florida. Plio-Pleistocene levels (designated Pp): Na, Nashua Formation of Florida. Pleistocene levels (designated Ps): Be, Bermont Formation of Florida.

the entire genus were compared using a Fisher's exact test to determine temporal variations in predation intensity (Table 7). Combined drilling frequencies were significantly higher in the Nashua Fm. than in the upper Pinecrest bed 3 of the Tamiami Formation (8.7% and 1.7% respectively, $p = 0.045$). Muricid drilling was significantly lower in the Bermont Fm. than in the Nashua Fm. (2.4% and 7.7% respectively, $p = 0.003$), and naticid drilling frequencies were significantly higher in the Bermont Fm. than in the Nashua Fm. (1.0% and 4.0% respectively, $p = 0.026$). Drilling frequencies on *Crepidula* species and the entire genus from the Atlantic Coastal Plain locality and the Gulf Coastal Plain locality of the Bermont Fm. were statistically compared for spatial variations in predation intensity, but showed no significant differences.

Prey Effectiveness

Yorktownian Localities

Muricid prey effectiveness (MPE) and combined prey effectiveness (CPE) values were calculated for *Crepidula* species and the entire genus from each Yorktownian locality (Table 8). The frequency of incomplete drillholes by muricids and a combination of muricids and naticids on the genus *Crepidula* was moderate in the middle Pliocene (0.385 and 0.192 respectively), steadily increased to extremely high levels in the late Pliocene (0.667 and 0.385), and returned to moderate levels in the Pleistocene (0.310 and 0.264, Figure 11a). Prey effectiveness values on the genus *Crepidula* were compared using a Fisher's exact test, and it was determined that the frequency of incomplete muricid drillholes was significantly higher in the first phase of the Waccamaw Fm. than in the James City Fm. ($p = 0.019$, Table 9).

The frequency of incomplete muricid and combined drillholes on the species *C. fornicata* followed a similar trend to the one seen for the entire genus (Figure 11b). A Fisher's exact comparison of prey effectiveness values on *C. fornicata* also showed that the frequency of incomplete muricid drillholes was significantly higher in the first phase of the Waccamaw Fm. than in the James City Fm. ($p = 0.020$, Table 10).

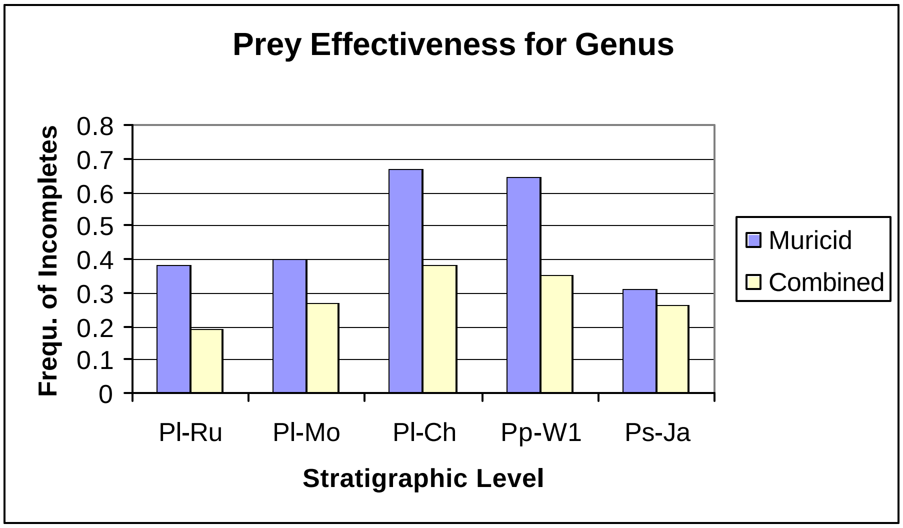
Muricid and combined prey effectiveness values on *C. fornicata* and the entire genus from the

| Formations | Drilled Specimens | | | Undrilled Specimens | | | Fisher's Exact prob. | | |
|---|---|---|---|---|---|---|---|---|---|
| | M | N | C | M | N | C | M | N | C |
| Bermont | 7 | 12 | 19 | 291 | 286 | 279 | | | |
| Nashua | 16 | 2 | 18 | 192 | 206 | 190 | 0.003* | 0.026* | 0.085 |
| | | | | | | | | | |
| Pinecrest | 1 | 0 | 1 | 57 | 58 | 57 | | | |
| Nashua | 16 | 2 | 18 | 192 | 206 | 190 | 0.068 | 0.611 | 0.045* |

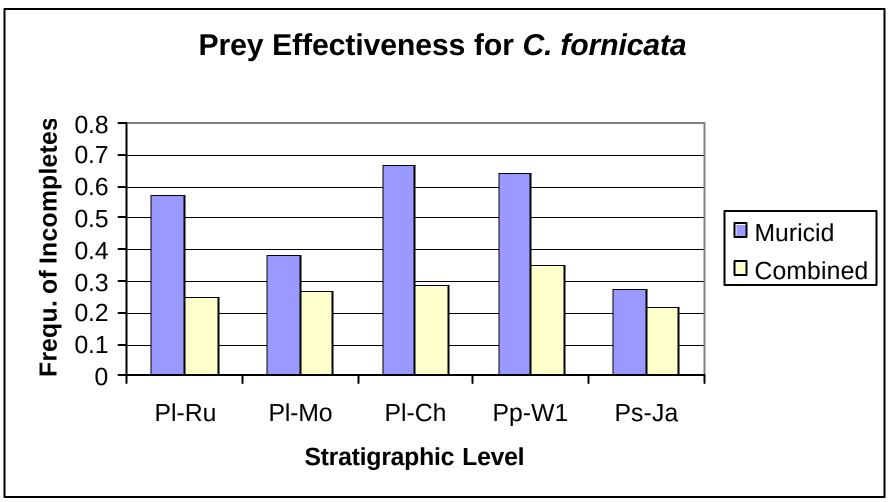
Table 7. Fisher's exact comparison of muricid (M), naticid (N), and combined (C) drilling frequencies on the genus *Crepidula* between stratigraphically successive formations of the Buckinghamian subprovince. Statistically significant differences ($p < 0.05$) are indicated with a (*).

| Locality (age) | Species | MPE | CPE |
|---|---|---|---|
| James City (E-Pleist) | *C. fornicata* | 0.276 | 0.216 |
| | *C. plana* | 0.25 | 0.25 |
| | *C. aculeata* | 0.36 | 0.323 |
| | Genus | 0.31 | 0.264 |
| 2nd Waccamaw (E-Pleist) | *C. fornicata* | 0.692 | 0.613 |
| | Genus | 0.692 | 0.594 |
| 1st Waccamaw (Plio-Pleist) | *C. fornicata* | 0.643 | 0.353 |
| | Genus | 0.643 | 0.353 |
| Chowan River (L-Plio) | *C. fornicata* | 0.667 | 0.286 |
| | *C. plana* | 0.5 | 0.333 |
| | Genus | 0.667 | 0.385 |
| Moore House (ML-Plio) | *C. fornicata* | 0.381 | 0.267 |
| | *C. aculeata* | 0.5 | 0.286 |
| | Genus | 0.4 | 0.27 |
| Rushmere (M-Plio) | *C. fornicata* | 0.571 | 0.25 |
| | *C. aculeata* | 0.167 | 0.1 |
| | Genus | 0.385 | 0.192 |
| Duplin (M-Plio) | *C. fornicata* | 0.308 | 0.313 |
| | Genus | 0.286 | 0.278 |
| Raysor (M-Plio) | *C. fornicata* | 0.571 | 0.364 |
| | *C. convexa* | 0.333 | 0.333 |
| | *C. aculeata* | 0.333 | 0.143 |
| | Genus | 0.462 | 0.286 |

Table 8. Compilation of muricid (MPE) and combined (CPE) prey effectiveness values for all *Crepidula* species (>20 specimens) at each Yorktownian locality. Localities and age are same as in Table 1.




a.




b.

Figure 11. a., b.) Prey effectiveness through time for the genus *Crepidula* (a.) and the species *C. fornicata* (b.) from selected Pliocene and Pleistocene localities of the Yorktownian molluscan subprovince. Abbreviations for stratigraphic levels are the same as in Figure 7.

| Formations | # Incomplete | | # Complete | | Fisher's Exact prob. | |
|---|---|---|---|---|---|---|
| | M | C | M | C | M | C |
| James City | 18 | 19 | 40 | 53 | | |
| 1st Waccamaw | 9 | 12 | 5 | 22 | 0.019* | 0.115 |
| | | | | | | |
| 1st Waccamaw | 9 | 12 | 5 | 22 | | |
| Chowan River | 4 | 5 | 2 | 8 | 0.387 | 0.257 |
| | | | | | | |
| Chowan River | 4 | 5 | 2 | 8 | | |
| Moore House | 10 | 10 | 15 | 27 | 0.185 | 0.199 |
| | | | | | | |
| Moore House | 10 | 10 | 15 | 27 | | |
| Rushmere | 5 | 5 | 8 | 21 | 0.272 | 0.188 |

Table 9. Fisher's exact comparison of muricid (M) and combined (C) prey effectiveness values on the genus *Crepidula* between stratigraphic successive formations of the Yorktownian subprovince. Statistically significant differences ($p < 0.05$) are indicated with a (*).

| Formations | # Incomplete | | # Complete | | Fisher's Exact prob. | |
|---|---|---|---|---|---|---|
| | M | C | M | C | M | C |
| James City | 8 | 8 | 21 | 29 | | |
| 1st Waccamaw | 9 | 12 | 5 | 22 | 0.020* | 0.094 |
| | | | | | | |
| 1st Waccamaw | 9 | 12 | 5 | 22 | | |
| Chowan River | 2 | 2 | 1 | 5 | 0.485 | 0.327 |
| | | | | | | |
| Chowan River | 2 | 2 | 1 | 5 | | |
| Moore House | 8 | 8 | 13 | 22 | 0.311 | 0.353 |
| | | | | | | |
| Moore House | 8 | 8 | 13 | 22 | | |
| Rushmere | 4 | 4 | 3 | 12 | 0.243 | 0.274 |

Table 10. Fisher's exact comparison of muricid (M) and combined (C) prey effectiveness values on the species *C. fornicata* between stratigraphic successive formations of the Yorktownian subprovince. Statistically significant differences ($p < 0.05$) are indicated with a (*).

Raysor Fm., the Duplin Fm., and the Rushmere Mbr. of the Yorktown Fm. were also compared using a Fisher's exact test to determine spatial variations in prey effectiveness. Prey effectiveness values between these correlative formations showed some variation; however, differences were not significant.

### Buckinghamian Localities

Muricid prey effectiveness (MPE) and combined prey effectiveness (CPE) values were calculated for *Crepidula* species and the entire genus for each of the four Buckinghamian localities (Table 11). The frequencies of muricid and combined incomplete drillholes on the entire genus were extremely high in the late Pliocene (0.75 and 0.80 respectively), and then decreased to moderately high levels at the Plio-Pleistocene boundary (0.469 and 0.441), and slightly increased into the Pleistocene (0.667 and 0.53, Figure 12a). Prey effectiveness values for *C. fornicata* showed a slightly different pattern than the one seen for the entire genus. The frequency of incomplete drillholes on *C. fornicata* decreased, as opposed to increased, into the Pleistocene (Figure 12b).

Prey effectiveness values from the upper Pinecrest bed 3 of the Tamiami Fm., the Nashua Fm., and the Bermont Fm. were statistically compared using a Fisher's exact test to determine temporal variations in prey effectiveness. Prey effectiveness values showed some variation through time, but differences were not statistically significant. Prey effectiveness values from the Atlantic and Gulf Coastal Plain localities of the Bermont Fm. were also statistically compared for spatial variations, but comparisons showed no significant differences.

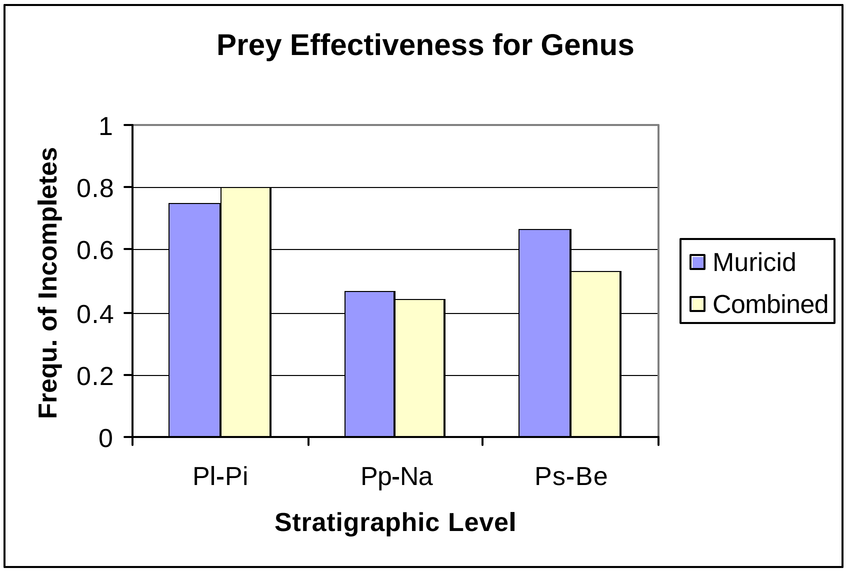
## Drillhole-site Selectivity

### Yorktownian Localities

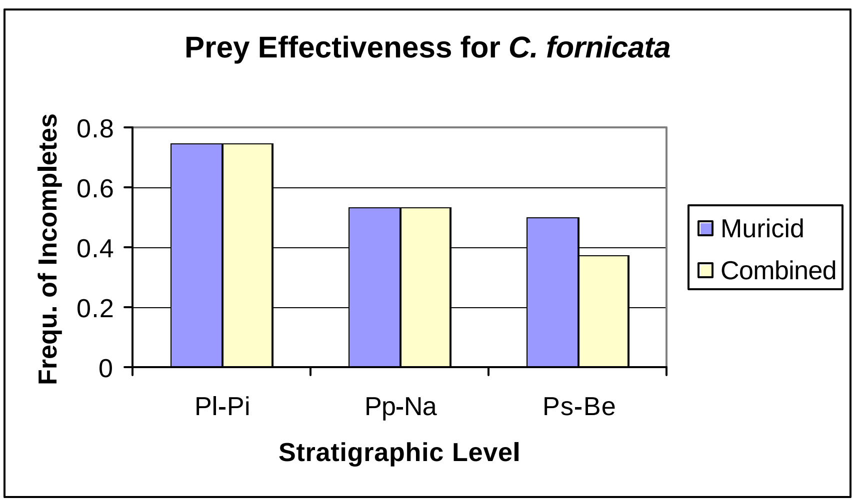
*Crepidula* specimens with complete muricid and naticid drillholes were surveyed from each Yorktownian locality for the study of drillhole-site selectivity. Pliocene localities and Pleistocene localities were combined so that a sufficient number of drillholes were present for statistical analysis. One species, *C. fornicata*, had enough drilled specimens to analyze statistically so

| Locality (age) | Species | MPE | CPE |
|---|---|---|---|
| Atl. Coast Bermont (Pleist) | *C. maculosa* | 0.6 | 0.615 |
| | *C. convexa* | 1 | 0.667 |
| | *C. aculeata* | 0.571 | 0.455 |
| | Genus | 0.611 | 0.543 |
| Gulf Coast Bermont (Pleist) | *C. fornicata* | 0.75 | 0.5 |
| | *C. maculosa* | 1 | 1 |
| | *C. convexa* | 1 | 1 |
| | *C. aculeata* | 0 | 0.333 |
| | Genus | 0.833 | 0.5 |
| Combined Bermont (Pleist) | *C. fornicata* | 0.5 | 0.375 |
| | *C. maculosa* | 0.667 | 0.643 |
| | *C. convexa* | 1 | 0.7 |
| | *C. aculeata* | 0.571 | 0.385 |
| | Genus | 0.667 | 0.533 |
| Nashua (Plio-Pleist) | *C. fornicata* | 0.536 | 0.536 |
| | Genus | 0.469 | 0.441 |
| Pinecrest Bed 3 (L-Plio) | *C. fornicata* | 0.75 | 0.8 |
| | Genus | 0.75 | 0.75 |

Table 11. Compilation of muricid (MPE) and combined (CPE) prey effectiveness values for all *Crepidula* species (>20 specimens) at each Buckinghamian locality.




a.




b.

Figure 12. a., b.) Prey effectiveness through time for the genus *Crepidula* (a.) and the species *C. fornicata* (b.) from Pliocene and Pleistocene localities of the Buckinghamian molluscan subprovince. Abbreviations for stratigraphic levels are same as in Figure 9.

*C. fornicata* and the entire *Crepidula* genus were surveyed for muricid and naticid drillhole-site stereotypy in the Pliocene and Pleistocene of the Yorktownian subprovince.

Yorktownian Pliocene localities included the Duplin Fm., the Raysor Fm., the Rushmere Mbr. and Moore House Mbr. of the Yorktown Fm., and the Chowan River Formation. Yorktownian Pleistocene localities included the first and second phases of the Waccamaw Fm. and the James City Formation. Table 12 shows the distribution of muricid and naticid drillholes by sector for *C. fornicata* and the entire genus as well as the significance of chi-squared tests. Tests show that muricids and naticids were highly selective with respect to the position of the drillhole on the prey's shell ($p < 0.05$ for all chi-squared tests). Analysis of drillhole position on *C. fornicata* and the entire genus showed that muricids and naticids exhibited strong site selectivity for sector 3 in both Pliocene and Pleistocene samples of the Yorktownian subprovince.

Buckinghamian Localities

*Crepidula* specimens with complete muricid and naticid drillholes were analyzed from each Buckinghamian locality for the study of drillhole-site stereotypy. Buckinghamian Pliocene localities included Bed 3 of the Pinecrest beds of the Tamiami Fm. and the Nashua Formation. Pleistocene localities included the Atlantic (near West Palm Beach, FL) and Gulf (near Naples, FL) Coastal sites of the Bermont Formation. There were no *Crepidula* species in the Buckinghamian localities that had a sufficient number of drilled specimens to analyze statistically, and naticid drillholes were present on only a few specimens collected from Pliocene samples. Therefore, the genus *Crepidula* was surveyed for muricid drillhole-site selectivity in the Pliocene and Pleistocene of the Buckinghamian subprovince, but was surveyed for naticid drillhole-site stereotypy only in the Pleistocene. Chi-squared tests indicate that muricids exhibited site selectivity for sector 1 on the genus *Crepidula* in Pliocene samples from the Buckinghamian subprovince, but were not site selective in Pleistocene samples (Table 12). Tests show that naticids were site selective for sector 3 on the genus *Crepidula* in Pleistocene samples of the Buckinghamian subprovince (Table 12).

| Subprovince | Age | Predator | Prey | Sector | | | | | Chi-Squared |
|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | |
| Yorktownian | Pleistocene | naticid | *C. fornicata* | 2 | 0 | 19 | 4 | 4 | 40.92 |
| Yorktownian | Pleistocene | naticid | Genus | 3 | 0 | 21 | 5 | 6 | 39.46 |
| Yorktownian | Pleistocene | muricid | *C. fornicata* | 4 | 4 | 18 | 3 | 5 | 24.19 |
| Yorktownian | Pleistocene | muricid | Genus | 5 | 6 | 32 | 4 | 6 | 55.42 |
| Yorktownian | Pliocene | naticid | *C. fornicata* | 2 | 3 | 19 | 4 | 0 | 43.23 |
| Yorktownian | Pliocene | naticid | Genus | 3 | 3 | 32 | 4 | 0 | 85.54 |
| Yorktownian | Pliocene | muricid | *C. fornicata* | 5 | 3 | 14 | 4 | 3 | 15.25 |
| Yorktownian | Pliocene | muricid | Genus | 7 | 4 | 19 | 7 | 5 | 17.93 |
| Buckinghamian | Pleistocene | muricid | Genus | 2 | 0 | 2 | 2 | 2 | 2.00 |
| Buckinghamian | Pleistocene | naticid | Genus | 2 | 1 | 10 | 0 | 0 | 26.63 |
| Buckinghamian | Pliocene | muricid | Genus | 11 | 0 | 6 | 0 | 1 | 18.65 |

Table 12. Frequency of muricid and naticid drillholes with respect to the five-sector grid superimposed on the prey's shell. Statistical comparison of drillhole-site selectivity using chi-squared tests. Values highlighted yellow are not significant at a level of $p < 0.05$.

Prey Species Selectivity

Yorktownian Localities

The relative abundances of each *Crepidula* species and the percentages of drilled specimens for each species were determined at every Yorktownian locality. Most of the *Crepidula* populations from Yorktownian localities were dominated by one or two species, with *C. fornicata* being the only species present in all eight of the localities (Table 13). *Crepidula fornicata* was usually one of the most dominant species within each locality representing anywhere from 29% (James City Fm.) to 100% (1st phase of the Waccamaw Fm.) of the total *Crepidula* population. The species *C. fornicata* was most frequently drilled by muricids in the James City Fm. (24.5% specimens drilled), and most frequently drilled by naticids in the Rushmere Mbr. of the Yorktown Fm. (20.5% specimens drilled). *Crepidula plana* was present in most localities except for the first phase of the Waccamaw Fm. and the Moore House Mbr. of the Yorktown Formation. *Crepidula convexa* was also absent from only two localities (the second phase of the Waccamaw Fm. and the James City Formation). *Crepidula plana* and *C. convexa* usually made up only a small percentage of the total *Crepidula* population. Both species represented only 1% of the total population in the Rushmere Mbr. of the Yorktown Fm. and the 2nd phase of the Waccamaw Formation. *Crepidula plana* reached its peak abundance of 36% in the Chowan River Fm., while *C. convexa* reached a high of 26% in the Raysor Formation. Neither *C. plana* nor *C. convexa* were frequently drilled by muricids or naticids. In populations containing more than 10 specimens of *C. plana* and *C. convexa* the highest percentage of individuals drilled by muricids was approximately 3% for *C. plana* (Chowan River Fm.) and 8% for *C. convexa* (Raysor and Duplin Fms.). The highest percentage of individuals drilled by naticids was 4% for *C. plana* (Duplin Fm.) and 6% for *C. convexa* (Chowan River Fm.). *Crepidula aculeata* was present in only four of the eight Yorktownian localities, including the Raysor Fm., the Rushmere Mbr. and the Moore House Mbr. of the Yorktown Fm., and the James City Formation; however, *C. aculeata* was fairly abundant in these formations. The relative abundance of *C. aculeata* was

| Locality | Species | # Spec. | # Dr. Spec. Mur | Nat | Rel. Ab. | % Dr. Spec. Mur | Nat |
|---|---|---|---|---|---|---|---|
| James City Fm, NC | *C. fornicata* | 53 | 13 | 8 | 29.4% | 24.5% | 15.1% |
| | *C. plana* | 7 | 1 | 0 | 3.9% | 14.3% | 0.0% |
| | *C. aculeata* | 120 | 13 | 5 | 66.7% | 10.8% | 4.2% |
| 2nd Waccamaw, NC | *C. fornicata* | 77 | 7 | 4 | 97.5% | 9.1% | 5.2% |
| | *C. plana* | 1 | 0 | 0 | 1.3% | 0.0% | 0.0% |
| | *C. convexa* | 1 | 0 | 1 | 1.3% | 0.0% | 100.0% |
| 1st Waccamaw, NC | *C. fornicata* | 138 | 5 | 15 | 100.0% | 3.6% | 10.9% |
| Chowan River Fm., VA | *C. fornicata* | 52 | 1 | 4 | 48.6% | 1.9% | 7.7% |
| | *C. plana* | 39 | 1 | 1 | 36.4% | 2.6% | 2.6% |
| | *C. convexa* | 16 | 0 | 1 | 15.0% | 0.0% | 6.3% |
| Moore House Mbr., VA | *C. fornicata* | 122 | 10 | 9 | 61.9% | 8.2% | 7.4% |
| | *C. convexa* | 6 | 0 | 0 | 3.0% | 0.0% | 0.0% |
| | *C. aculeata* | 69 | 2 | 3 | 35.0% | 2.9% | 4.3% |
| Rushmere Mbr., VA | *C. fornicata* | 44 | 3 | 9 | 41.1% | 6.8% | 20.5% |
| | *C. plana* | 1 | 0 | 0 | 0.9% | 0.0% | 0.0% |
| | *C. convexa* | 1 | 0 | 0 | 0.9% | 0.0% | 0.0% |
| | *C. aculeata* | 61 | 5 | 3 | 57.0% | 8.2% | 4.9% |
| Duplin Fm., NC | *C. fornicata* | 66 | 7 | 2 | 65.3% | 10.6% | 3.0% |
| | *C. plana* | 23 | 0 | 1 | 22.8% | 0.0% | 4.3% |
| | *C. convexa* | 12 | 1 | 0 | 11.9% | 8.3% | 0.0% |
| Raysor Fm., SC | *C. fornicata* | 45 | 2 | 4 | 47.9% | 4.4% | 8.9% |
| | *C. plana* | 3 | 0 | 0 | 3.2% | 0.0% | 0.0% |
| | *C. convexa* | 24 | 2 | 0 | 25.5% | 8.3% | 0.0% |
| | *C. aculeata* | 22 | 1 | 4 | 23.4% | 4.5% | 18.2% |

Table 13. Relative abundances and percentage of specimens drilled by muricids and naticids for *Crepidula* species from each Yorktownian locality.

lowest in the Raysor Fm., representing 23% of the total *Crepidula* population, and it was highest in the James City Formation, representing 67% of the total population. The species *C. aculeata* was most frequently drilled by muricids in the James City Fm. (11%), and was most frequently drilled by naticids in the Raysor Fm. (18%).

Buckinghamian Localities

All of the four Buckinghamian localities had at least two and no more than five species of *Crepidula* present (Table 14). *Crepidula fornicata* was the only species present within each of the four localities, and was the dominant species in both the Pinecrest bed 3 of the Tamiami Fm. and the Nashua Formation. *Crepidula fornicata* was most abundant in the Pinecrest beds, representing 91% of the total *Crepidula* population, and was least abundant in the Atlantic Coastal Plain locality of the Bermont Formation, representing just 6% of the population; however, despite its relatively low abundance, *C. fornicata* from this locality were more frequently drilled by muricids (17%) than in the other three Buckinghamian localities. *Crepidula fornicata* from the Gulf Coastal Plain locality of the Bermont Fm. were more frequently drilled by naticids than in the other three Buckinghamian localities. *Crepidula plana* was present in two of the localities, representing 1% of the population in the Gulf Coastal Plain locality of the Bermont Fm. and 11% of the population in the Nashua Formation. Approximately 5% of the specimens of *C. plana* from the Nashua Fm. were drilled by muricids, which was the only locality to contain any individuals drilled by muricids or naticids. *Crepidula convexa* was present in three localities and was the dominant species in the Atlantic Coastal Plain locality of the Bermont Formation, representing 39% of the *Crepidula* population. *Crepidula convexa* was least abundant in the Gulf Coastal Plain locality of the Bermont Formation, representing 17% of the population. *Crepidula convexa* was most frequently drilled by naticids in the Atlantic Coastal Plain locality of the Bermont Formation, and was most frequently drilled by muricids in the Nashua Fm. (approximately 4% and 6% respectively). *Crepidula aculeata* occurred in both localities of the Bermont Formation, representing 28% of the population in the Atlantic Coastal Plain locality, and

| Locality | Species | # Spec. | # Dr. Spec. Mur | Nat | Rel. Ab. | % Dr. Spec. Mur | Nat |
|---|---|---|---|---|---|---|---|
| Bermont Fm. (Atl.), FL | *C. fornicata* | 12 | 2 | 0 | 5.8% | 16.7% | 0.0% |
| | *C. plana* | 0 | 0 | 0 | 0.0% | NA | NA |
| | *C. convexa* | 81 | 0 | 3 | 39.1% | 0.0% | 3.7% |
| | *C. aculeata* | 59 | 3 | 3 | 28.5% | 5.1% | 5.1% |
| | *C. maculosa* | 55 | 1 | 3 | 26.6% | 1.8% | 5.5% |
| Bermont Fm. (Gulf), FL | *C. fornicata* | 11 | 1 | 2 | 12.1% | 9.1% | 18.2% |
| | *C. plana* | 1 | 0 | 0 | 1.1% | 0.0% | 0.0% |
| | *C. convexa* | 15 | 0 | 0 | 16.5% | 0.0% | 0.0% |
| | *C. aculeata* | 43 | 0 | 1 | 47.3% | 0.0% | 2.3% |
| | *C. maculosa* | 21 | 0 | 0 | 23.1% | 0.0% | 0.0% |
| Bermont Fm. (combined), FL | *C. fornicata* | 23 | 3 | 2 | 7.7% | 13.0% | 8.7% |
| | *C. plana* | 1 | 0 | 0 | 0.3% | 0.0% | 0.0% |
| | *C. convexa* | 96 | 0 | 3 | 32.2% | 0.0% | 3.1% |
| | *C. aculeata* | 102 | 3 | 4 | 34.2% | 2.9% | 3.9% |
| | *C. maculosa* | 76 | 1 | 3 | 25.5% | 1.3% | 3.9% |
| Nashua Fm., FL | *C. fornicata* | 138 | 12 | 1 | 66.3% | 8.7% | 0.7% |
| | *C. plana* | 22 | 1 | 0 | 10.6% | 4.5% | 0.0% |
| | *C. convexa* | 48 | 3 | 1 | 23.1% | 6.3% | 2.1% |
| Pinecrest Beds (3), FL | *C. fornicata* | 53 | 1 | 0 | 91.4% | 1.9% | 0.0% |
| | *C. maculosa* | 5 | 0 | 0 | 8.6% | 0.0% | 0.0% |

Table 14. Relative abundances and percentage of specimens drilled by muricids and naticids for *Crepidula* species from each Buckinghamian localities.

was the dominant *Crepidula* species on the Gulf Coastal Plain locality, representing 47% of the population. *Crepidula aculeata* from the Atlantic Coastal Plain locality of the Bermont Fm. were more frequently drilled by muricids and naticids (5% for both) than in the other three localities. *Crepidula maculosa* was present in three of the localities, including bed 3 of the Pinecrest Beds, and both localities of the Bermont Formation. *Crepidula maculosa* represented 9% of the *Crepidula* population in bed 3 of the Pinecrest Beds, 27% of the population in the Bermont Fm. from the Atlantic Coastal Plain, and 23% of the population in the Bermont Fm. from the Gulf Coastal Plain. The Atlantic Coastal Plain locality of the Bermont Fm. contained the only individuals of *C. maculosa* that were drilled by naticids or muricids (6% and 2% respectively).

Statistical comparisons of percentages of drilled specimens between *Crepidula* species from each locality indicated that naticids exhibited species selectivity in two Yorktownian localities, but were not species selective in any of the Buckinghamian localities. Tests show that muricids exhibited species selectivity in one Yorktownian locality and one Buckinghamian formation.

Naticids drilled *C. fornicata* more frequently than *C. aculeata* in both the Rushmere Mbr. of the Yorktown Fm. and the James City Formation, despite the fact that *C. aculeata* was more abundant in both localities. Comparisons between the percentages of drilled specimens for *C. fornicata* and *C. aculeata* from the Rushmere Mbr. of the Yorktown Fm. and the James City Fm. showed that differences were statistically significant ($p = 0.01$ at both localities, Table 15).

Muricids also drilled *C. fornicata* more frequently than *C. aculeata* in the James City Formation. Comparisons between percentages of drilled specimens for *C. fornicata* and *C. aculeata* showed that differences were statistically significant ($p = 0.01$, Table 15). Muricids did not exhibit species selectivity in any of the four Buckinghamian localities; however, comparing specimens of *C. fornicata* and *C. maculosa* from both localities of the Bermont Fm. showed that differences in the percentage of individuals drilled between these species were statistically significant ($p = 0.03$, Table 15).

| Locality | Species | # Spec. | # Dr. Spec. | | # Un. Spec. | | Fisher's ex. prob. | |
|---|---|---|---|---|---|---|---|---|
| | | | M | N | M | N | M | N |
| Bermont Fm. (both loc.), FL | *C. fornicata* | 23 | 3 | 2 | 20 | 21 | p = 0.03* | p = 0.25 |
| | *C. maculosa* | 76 | 1 | 3 | 75 | 73 | | |
| James City Fm., Aurora, NC | *C. fornicata* | 53 | 13 | 8 | 40 | 45 | p = 0.01* | p = 0.01* |
| | *C. aculeata* | 120 | 13 | 5 | 107 | 115 | | |
| Rushmere Mbr., Lt. Run, VA | *C. fornicata* | 44 | 3 | 9 | 41 | 35 | p = 0.28 | p = 0.01* |
| | *C. aculeata* | 61 | 5 | 3 | 56 | 58 | | |

Table 15. Localities that showed muricid and/or naticid selectivity with respect to *Crepidula* species. Statistically significant differences ($p < 0.05$) are indicated with a (*).

Prey Size Selectivity

Histograms showing size distributions of individual specimens collected from each locality were generated for each *Crepidula* species and the entire genus. Histograms showed the total number of specimens whose shell length was within a particular size range, and the number of specimens within each size range that contained complete muricid or naticid drillholes. The proportion of drilled specimens within each size class was compared statistically using a Fisher's exact test.

Muricids exhibited size selectivity on *Crepidula* specimens from two localities, the 2nd phase of the Waccamaw Fm. and the James City Formation. Size frequency histograms of *C. fornicata* and the genus *Crepidula* from the 2nd phase of the Waccamaw Fm. show that approximately 40% of the specimens were 25-35mm in size and 27% of the specimens were 35-45mm in size making them the two dominant size classes (Figure 13). However, muricids drilled 19% of the specimens that were 25-35mm in size, and 0% of the specimens that were 35-45mm in size. A Fisher's exact comparison of muricid drillholes between these size classes indicated that differences were statistically significant ($p = 0.03$, Table 16), suggesting that muricids selected *Crepidula* that were 25-35mm in size over specimens 35-45mm in size.

Size frequency histograms of *C. fornicata* from the James City Fm. also shows that the two dominant size classes are 25-35mm and 35-45mm, containing 51% and 30% of the specimens respectively (Figure 14). Muricids drilled approximately 44% of the specimens that were 35-45mm in size and only about 15% of the specimens that were 25-35mm in size. A Fisher's exact comparison between these size classes shows that muricids selected *C. fornicata* 35-45mm in size over those 25-35mm in size ($p = 0.035$, Table 16).

Size frequency histograms of the genus *Crepidula* from the James City Fm. shows that 56% of the specimens are 15-25mm in size, 28% of the specimens are 25-35mm in size, and 12% of the specimens are 35-45mm in size (Figure 14). Muricids drilled about 14% of the specimens 15-25mm in size, 8% of the specimens 25-35mm in size, and 38% of the specimens 35-45mm in

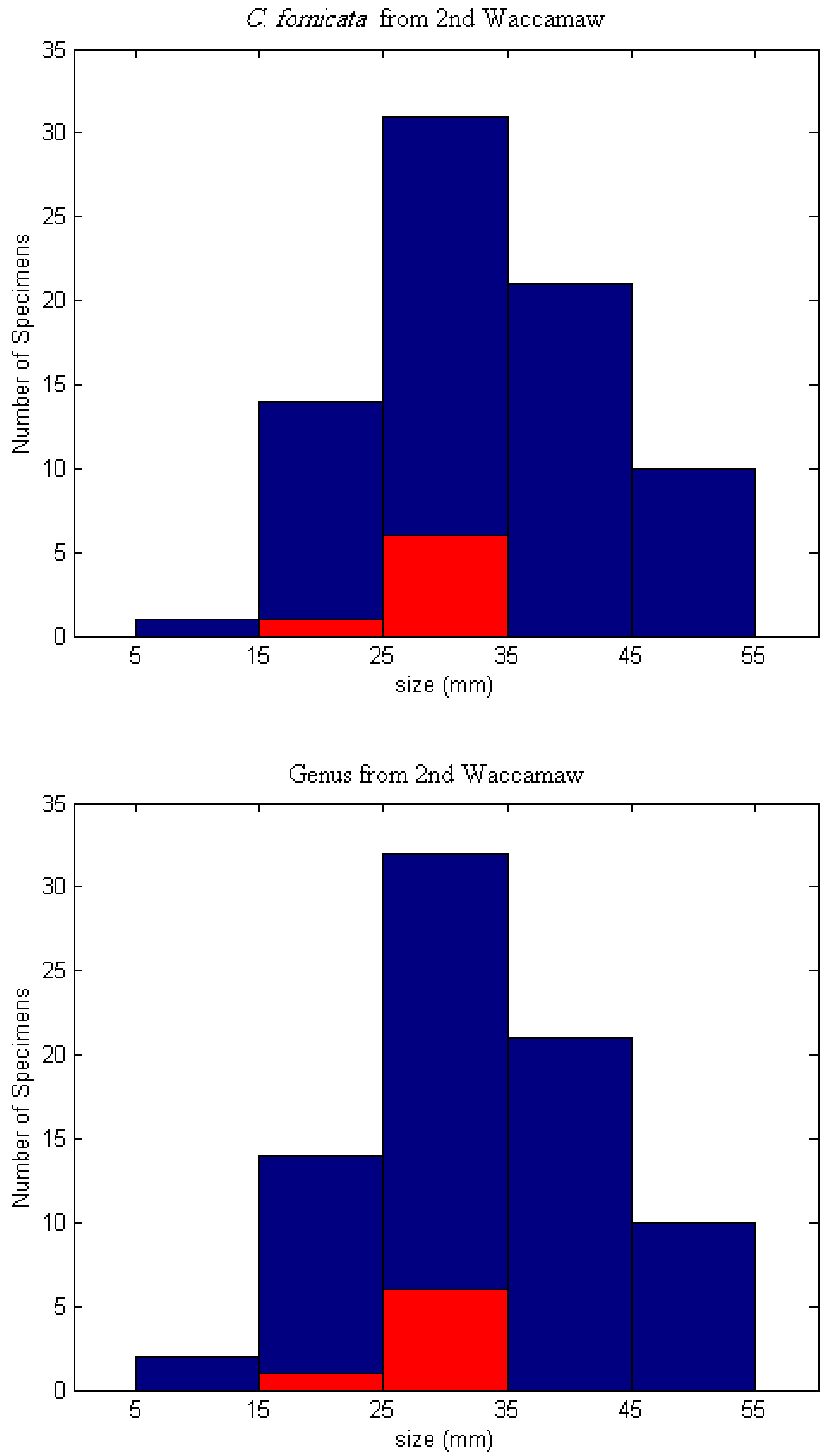
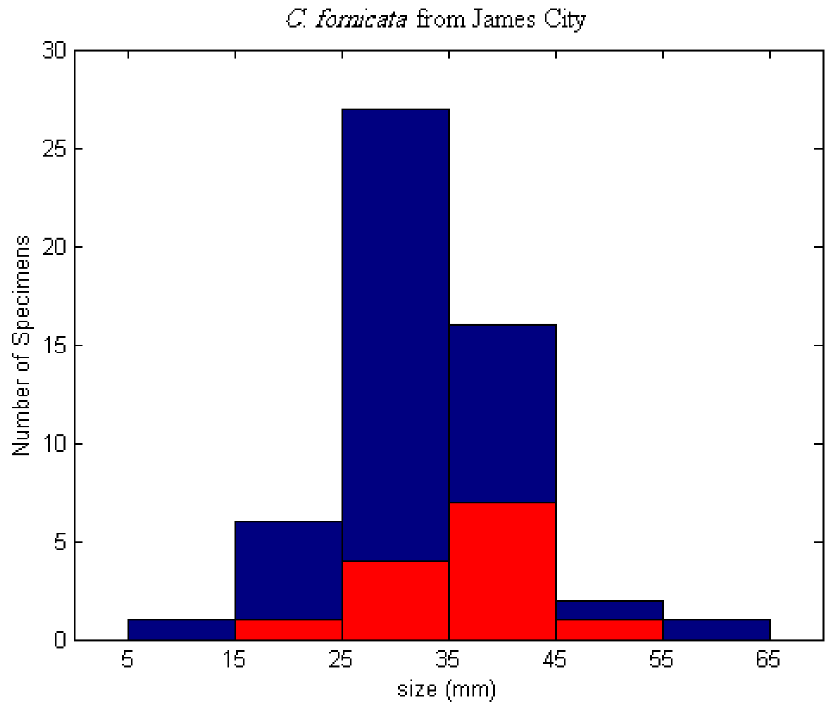



Figure 13. Size frequency distributions of *Crepidula fornicata* (top) and the genus *Crepidula* (bottom) from the 2$^{nd}$ phase of the Waccamaw Formation, Shallotte, NC. Red bars represent the number of specimens in that size range with one or more complete muricid drillhole.

| **Locality** | **Pred.** | **Prey** | **Prey Sz.** | **# Spec.** | **# Dr.** | **# Un.** | **% Dr.** | **Probability** |
|---|---|---|---|---|---|---|---|---|
| James City | muricid | *C. fornicata* | 25-35mm | 27 | 4 | 23 | 14.8% | p = 0.035 |
| | | | 35-45mm | 16 | 7 | 9 | 43.8% | |
| James City | muricid | Genus | 15-25mm | 102 | 14 | 88 | 13.7% | p = 0.010 |
| | | | 35-45mm | 21 | 8 | 13 | 38.1% | |
| James City | muricid | Genus | 25-25mm | 51 | 4 | 47 | 7.8% | p = 0.003 |
| | | | 35-45mm | 21 | 8 | 13 | 38.1% | |
| 2nd Wacc. | muricid | *C. fornicata* | 25-35mm | 31 | 6 | 25 | 19.4% | p = 0.032 |
| | | | 35-45mm | 21 | 0 | 21 | 0.0% | |
| 2nd Wacc. | muricid | Genus | 25-35mm | 32 | 6 | 26 | 18.8% | p = 0.039 |
| | | | 35-45mm | 21 | 0 | 21 | 0.0% | |
| Rushmere | naticid | *C. fornicata* | 25-35mm | 16 | 0 | 16 | 0.0% | p = 0.004 |
| | | | 35-45mm | 17 | 7 | 10 | 41.2% | |
| Rushmere | naticid | Genus | 25-35mm | 41 | 1 | 40 | 2.4% | p = 0.006 |
| | | | 35-45mm | 34 | 8 | 26 | 23.5% | |

Table 16. Localities that showed muricid and naticid selectivity of *Crepidula fornicata* and the genus *Crepidula* with respect to specimen size.



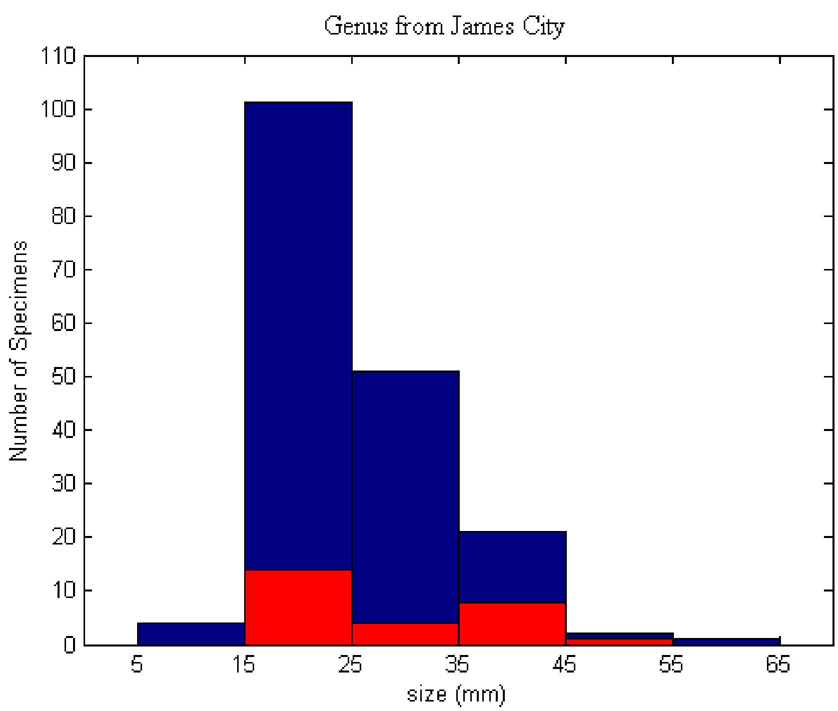




Figure 14. Size frequency distributions of *Crepidula fornicata* (top) and the genus *Crepidula* (bottom) from the James City Formation, Aurora, NC. Red bars represent the number of specimens in that size range with one or more complete muricid drillhole.

size. A Fisher's exact comparison between these size classes indicates that muricids selected *Crepidula* 35-45mm in size over those 15-25mm and 25-35mm in size (p = 0.01 and p = 0.003 respectively, Table 16).

Naticids exhibited size selectivity on *Crepidula* specimens from only one locality, the Rushmere Mbr. of the Yorktown Formation. Size frequency histograms of *C. fornicata* from this locality show that 16% of the specimens are 15-25mm in size, 36% of the specimens are 25-35mm in size, and 39% of the specimens are 35-45mm in size (Figure 15). Naticids drilled approximately 29% of the specimens 15-25mm in size and 41% of the specimens 35-45mm in size; however, none of the specimens 25-35mm in size were drilled by naticids. A Fisher's exact comparison between these size classes indicates that naticids selected specimens 35-45mm in size over specimens 25-35mm in size (p = 0.004, Table 16).

Size frequency histograms of the genus *Crepidula* from the Rushmere Mbr. of the Yorktown Fm. showed that 24% of the specimens are 15-25mm in size, 38% of the specimens are 25-35mm in size, and 32% of the specimens are 35-45mm in size (Figure 15). Naticids drilled 12% of the specimens 15-25mm in size and 24% of those 35-45mm in size, but only 2% of the specimens 25-35mm in size were drilled by naticids. Statistical comparison between these size classes shows that naticids selected specimens 35-45mm over 25-35mm in size (p = 0.006, Table16).

Size frequency histograms of *Crepidula* from the other localities in this study indicated that muricids and naticids were not selective with respect to prey size. In some cases the number of muricid and naticid prey specimens within each size class was directly proportional to the total number of specimens from each size class (Figure 16). In many cases muricid and naticid prey were randomly distributed between size classes (Figure 16), indicating that specimen size had little, if any, influence in determining muricid and naticid prey selection.

Spatial Comparisons: Yorktownian vs. Buckinghamian

Predation Intensity

Muricid, naticid, and combined drilling frequencies from the four Buckinghamian localities

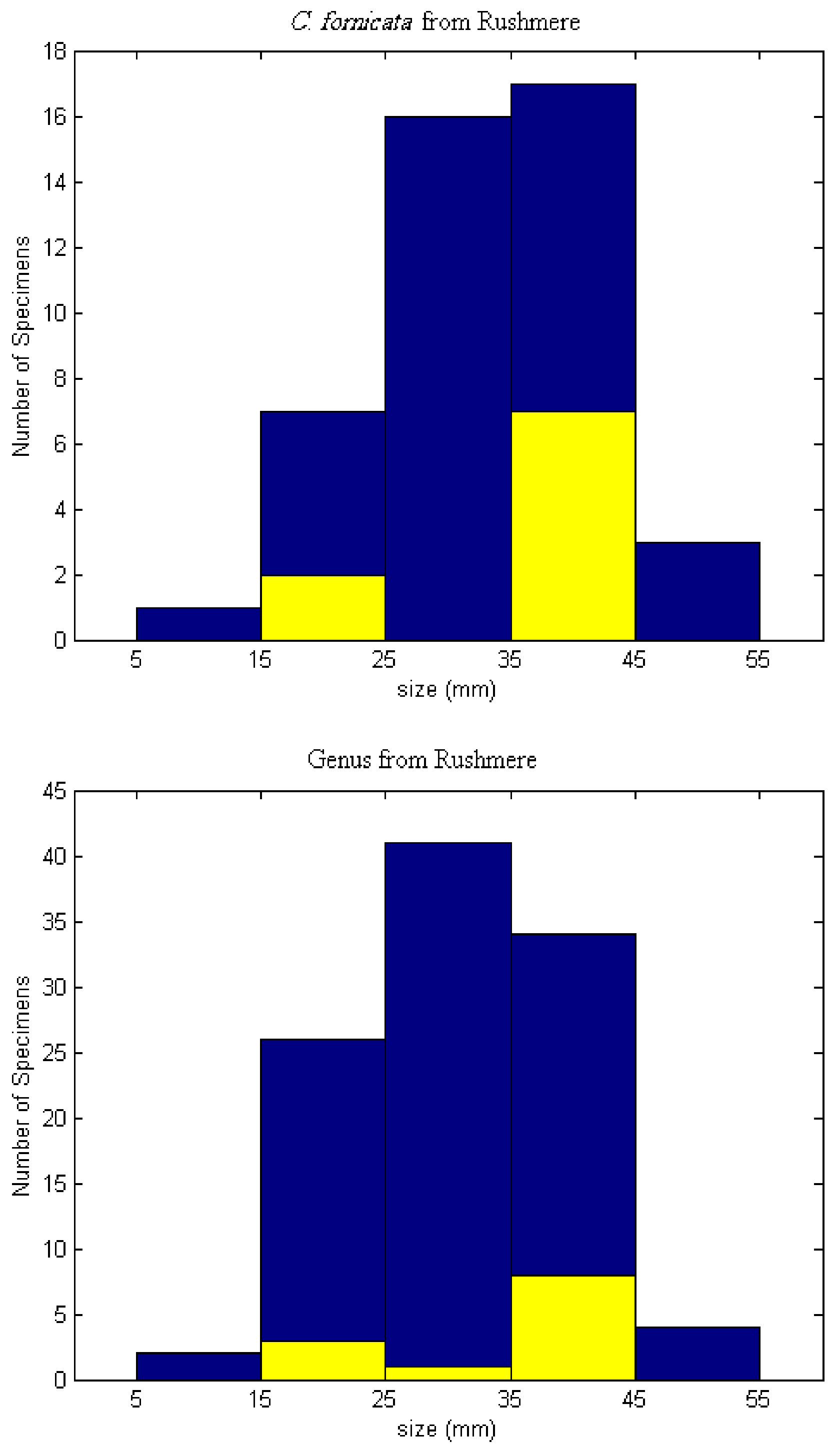



Figure 15. Size frequency distributions of *Crepidula fornicata* (top) and the genus *Crepidula* (bottom) from the Rushmere Member of the Yorktown Formation, Lt. Run, NC. Yellow bars represent the number of specimens in that size range with one or more complete naticid drillhole.

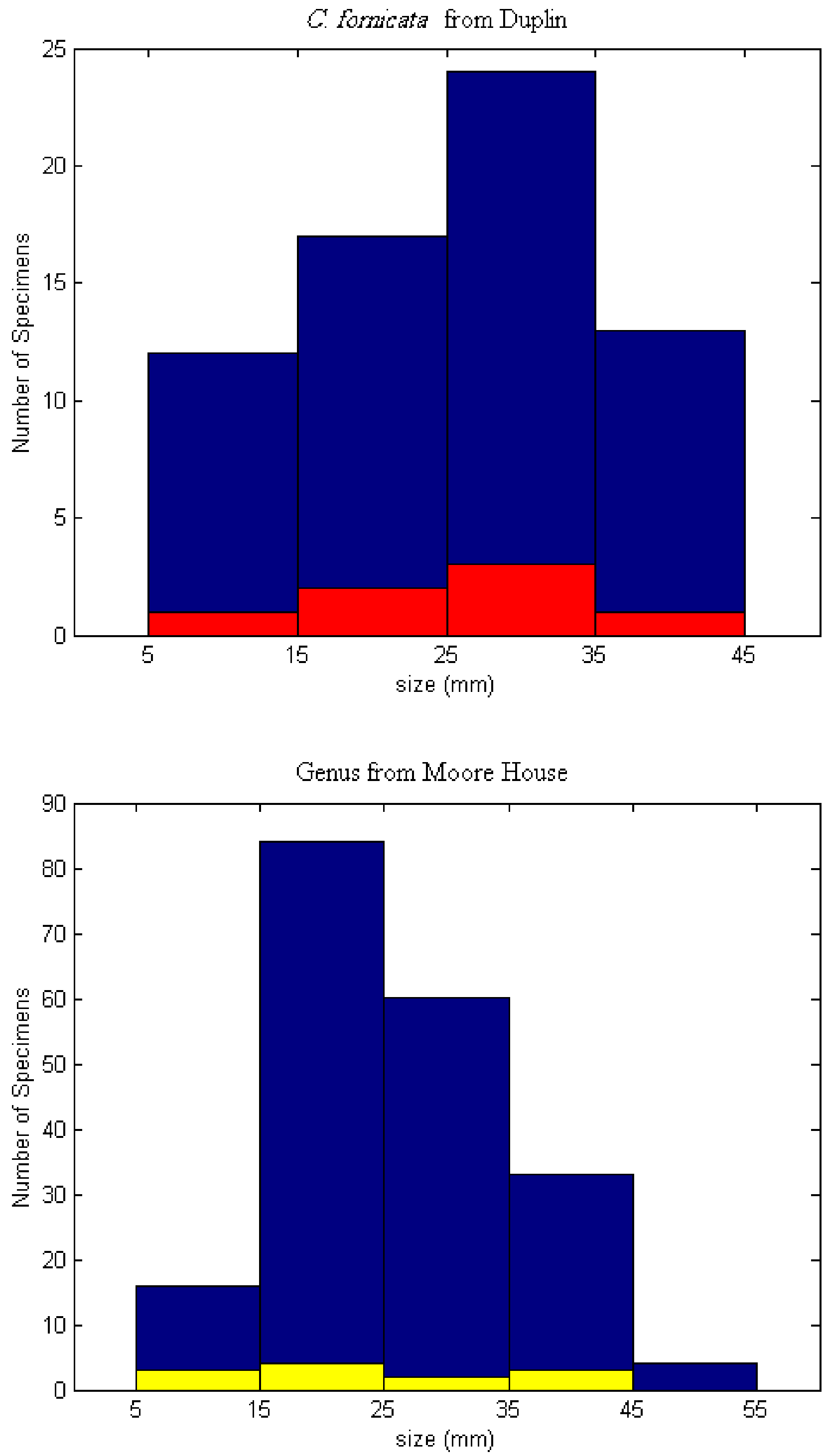
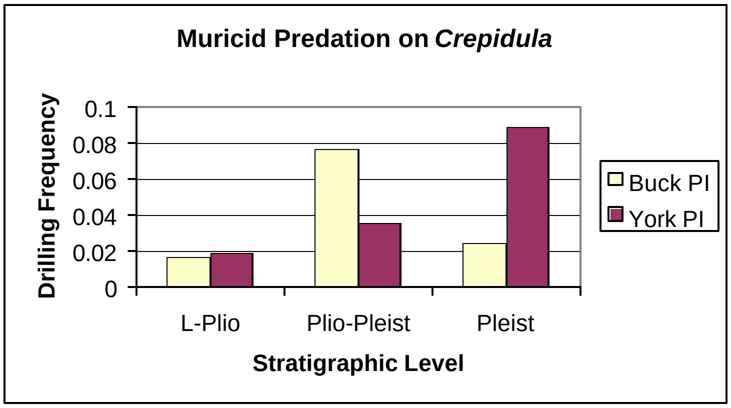



Figure 16. Size frequency distributions of *C. fornicata* (top) and the genus *Crepidula* (bottom) from the Duplin Fm. and the Moore House Mbr. of the Yorktown Fm. Red (muricid) and yellow (naticid) bars represent the number of specimens in that size range with complete drillholes.

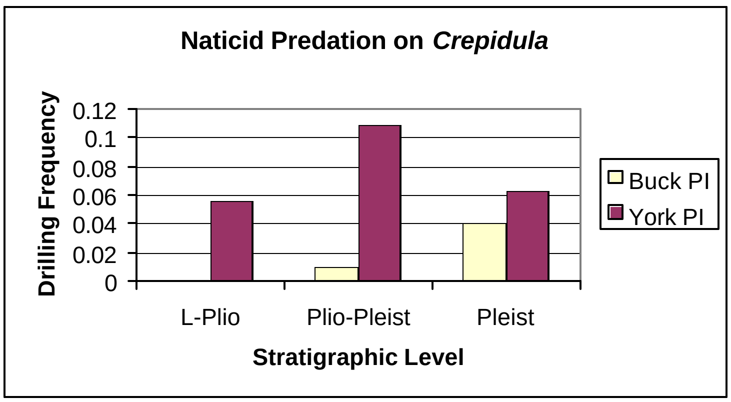
were compared statistically to drilling frequencies from several correlative Yorktownian localities using a Fisher's exact test to determine spatial variations in predation intensity. Bed 3 of the upper Pinecrest Beds of the Tamiami Fm. (late Pliocene) was compared to the Chowan River Fm. (late Pliocene), the Nashua Fm. (Plio-Pleistocene) was compared to the first phase of the Waccamaw Fm. (Plio-Pleistocene), and the Bermont Fm. (Pleistocene) was compared to the second phase of the Waccamaw Fm. (Pleistocene).

Muricid drilling frequencies on the genus *Crepidula* were similarly low in both the Pinecrest Beds (1.7%) and the Chowan River Fm. (1.9%, Figure 17a). Muricid drilling was higher in the Nashua Fm. (7.7%) than in the first phase of the Waccamaw Fm. (3.6%), but differences were not statistically significant (Table 17). In the Pleistocene muricid drilling was significantly higher in the second phase of the Waccamaw Fm. than in the Bermont Fm. (8.9% and 2.4% respectively, $p = 0.011$). Naticid and combined drilling frequencies on *Crepidula* from these localities showed a similar trend. Naticid and combined drilling was more intense in the three Yorktownian localities than in the correlative Buckinghamian localities (Figure 17b,c). Naticid and combined drilling frequencies in the first phase of the Waccamaw Fm. (10.9% and 14.5% respectively) were significantly higher than in the Nashua Fm. (1% and 8.7%, $p = 0.000$ and 0.033 respectively). Combined drilling frequencies in the second phase of the Waccamaw Fm. (15.2%) were also significantly higher than in the Bermont Fm. (6.4%, $p = 0.008$).

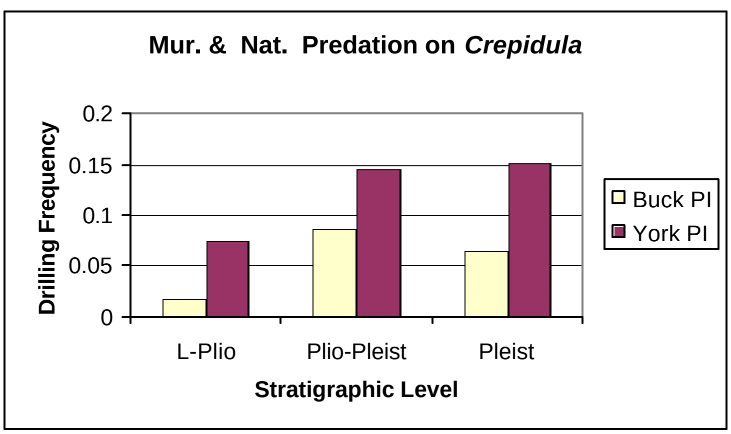
Muricid drilling on *C. fornicata* was equally low in both the Pinecrest Beds (1.9%) and the Chowan River Fm. (1.9%, Figure 18a). Muricid drilling was more intense in the Nashua Fm. (8.7%) than the first phase of the Waccamaw Fm. (3.6%), and comparisons showed the difference to be statistically significant ($p = 0.044$, Table 18). Muricid drilling on *C. fornicata* in the Pleistocene was also higher in the Bermont Fm. (13.0%) than in the second phase of the Waccamaw Fm. (9.1%), but the difference was not statistically significant. Naticid and combined drilling frequencies on *C. fornicata* were higher in the Chowan River Fm. (7.7% and 9.6% respectively) than in the Pinecrest Beds (0% and 1.9%, Figure 18b,c), but differences were not




a.




b.

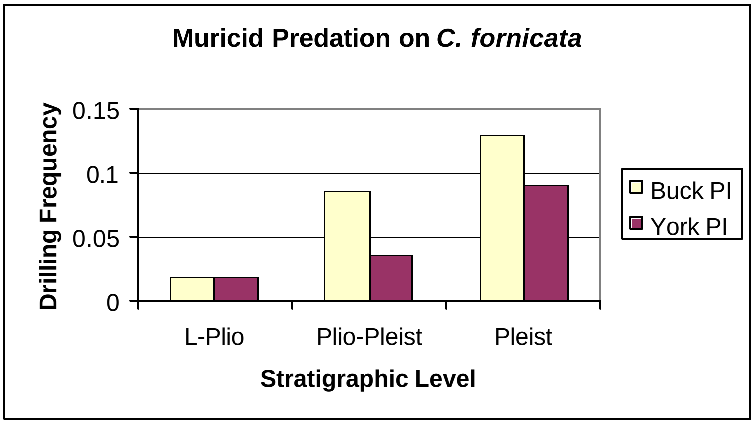



c.

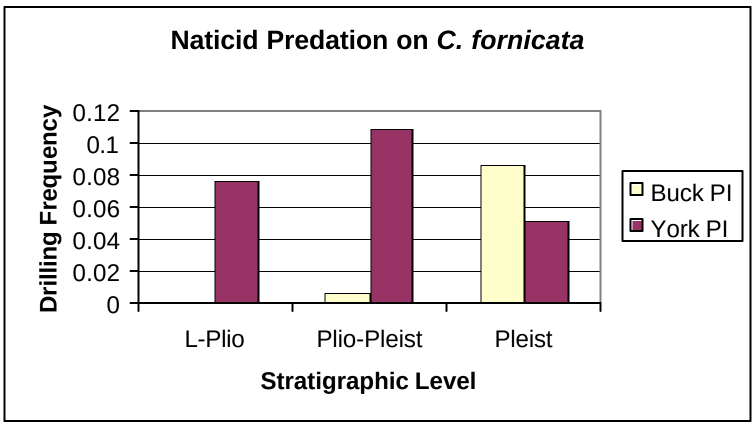
Figure 17. a., b., c.) Muricid (a.), naticid (b.), and combined (c.) drilling frequencies on the genus *Crepidula* from correlative localities of the Yorktownian and Buckinghamian subprovince. Buckinghamian localities; L-Plio, Pinecrest bed 3; Plio-Pleist, Nashua Fm.; Pleist, Bermont; Yorktownian localities; L-Plio, Chowan River Fm.; Plio-Pleist, 1st Waccamaw; Pleist, 2nd Waccamaw.

| Formations | Drilled Specimens | | | Undrilled Specimens | | | Fisher's Exact prob. | | |
|---|---|---|---|---|---|---|---|---|---|
| | M | N | C | M | N | C | M | N | C |
| Pinecrest | 1 | 0 | 1 | 57 | 58 | 57 | 0.474 | 0.071 | 0.095 |
| Chowan River | 2 | 6 | 8 | 105 | 101 | 99 | | | |
| Nashua | 16 | 2 | 18 | 192 | 206 | 190 | 0.057 | 0.000* | 0.033* |
| 1st Waccamaw | 5 | 15 | 20 | 133 | 123 | 118 | | | |
| Bermont | 7 | 12 | 19 | 291 | 286 | 279 | 0.011* | 0.151 | 0.008* |
| 2nd Waccamaw | 7 | 5 | 12 | 72 | 74 | 65 | | | |

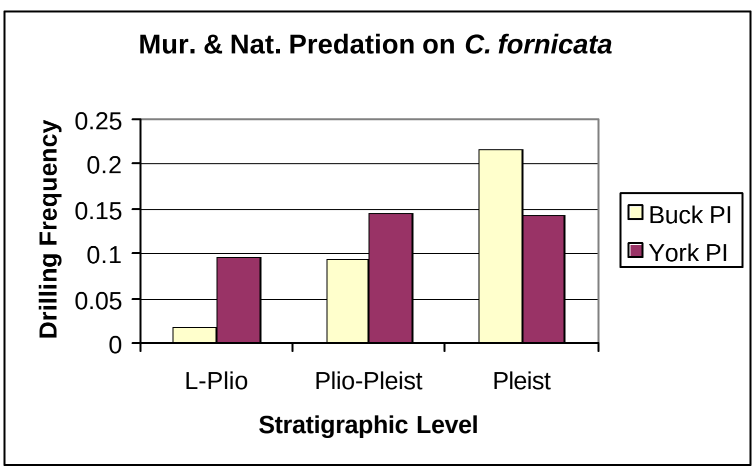
Table 17. Fisher's exact comparison of muricid (M), naticid (N), and combined (C) drilling frequencies on the genus *Crepidula* between correlative localities of the Buckinghamian and Yorktownian subprovinces. Statistically significant differences ($p < 0.05$) are indicated with a (*).




a.




b.




c.

Figure 18. a., b., c.) Muricid (a.), naticid (b.), and combined (c.) drilling frequencies on *C. fornicata* from correlative localities of the Yorktownian and Buckinghamian subprovince. Buckinghamian localities; L-Plio, Pinecrest bed 3; Plio-Pleist, Nashua Fm.; Pleist, Bermont; Yorktownian localities; L-Plio, Chowan River Fm.; Plio-Pleist, 1st Waccamaw; Pleist, 2nd Waccamaw.

| Formations | Drilled Specimens | | | Undrilled Specimens | | | Fisher's Exact prob. | | |
|---|---|---|---|---|---|---|---|---|---|
| | M | N | C | M | N | C | M | N | C |
| Pinecrest | 1 | 0 | 1 | 52 | 53 | 52 | 0.505 | 0.057 | 0.086 |
| Chowan River | 1 | 4 | 5 | 51 | 48 | 47 | | | |
| Nashua | 12 | 1 | 13 | 126 | 137 | 125 | 0.044* | 0.000* | 0.064 |
| 1st Waccamaw | 5 | 15 | 20 | 133 | 123 | 118 | | | |
| Bermont | 3 | 2 | 5 | 20 | 21 | 18 | 0.246 | 0.287 | 0.167 |
| 2nd Waccamaw | 7 | 4 | 11 | 70 | 73 | 66 | | | |

Table 18. Fisher's exact comparison of muricid (M), naticid (N), and combined (C) drilling frequencies on the species *C. fornicata* between correlative localities of the Buckinghamian and Yorktownian subprovinces. Statistically significant differences ($p < 0.05$) are indicated with a (*).

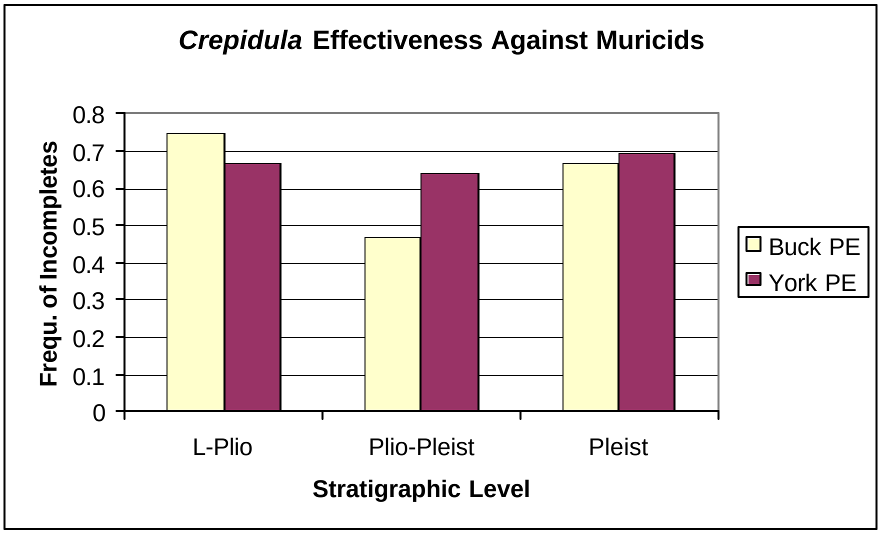
statistically significant. Naticid and combined drilling was also more intense in the first phase of the Waccamaw Fm. (10.9% and 14.5%) than in the Nashua Fm. (0.7% and 9.4%), and comparisons showed that the difference in naticid drilling was statistically significant (p = 0.000). However, in the Pleistocene naticid and combined drilling on *C. fornicata* is more intense in the Bermont Fm. (8.7% and 21.7% respectively) than in the second phase of the Waccamaw Fm. (5.2% and 14.3%), but these differences are not statistically significant.

Prey Effectiveness

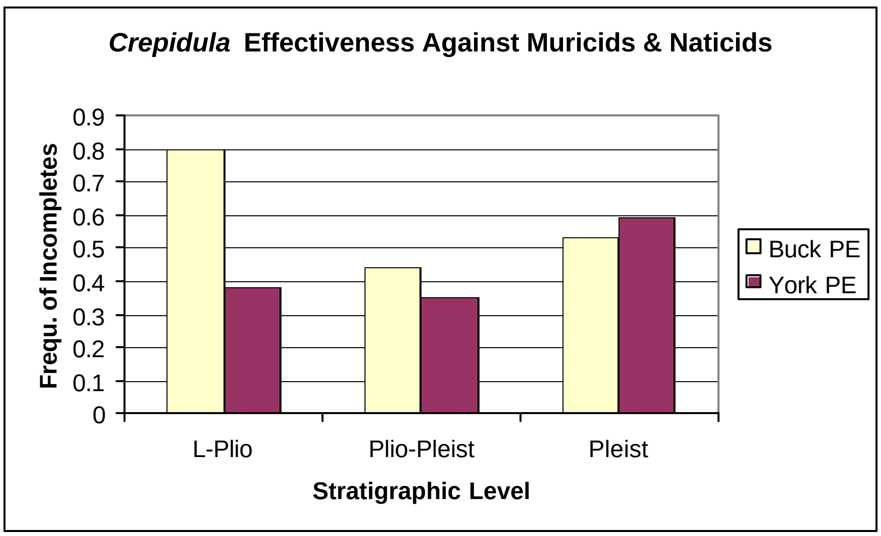
Muricid and combined prey effectiveness values from the four Buckinghamian localities were compared to prey effectiveness values from several correlative Yorktownian localities to determine spatial variations in prey efficiency. Bed 3 of the upper Pinecrest Beds of the Tamiami Fm. (late Pliocene) was compared to the Chowan River Fm. (late Pliocene), the Nashua Fm. (Plio-Pleistocene) was compared to the first phase of the Waccamaw Fm. (Plio-Pleistocene), and the Bermont Fm. (Pleistocene) was compared to the second phase of the Waccamaw Fm. (Pleistocene).

The frequency of incomplete muricid drillholes on the genus *Crepidula* was slightly higher in the Pinecrest Beds (0.75) than in the Chowan River Fm. (0.667, Figure 19a). The frequency of incomplete muricid drillholes on the genus was slightly lower in the Nashua Fm. (0.469) and Bermont Fm. (0.667) than in the correlative first phase of the Waccamaw Fm. (0.643) and second phase of the Waccamaw Fm. (0.692, Figure 19a). The frequency of combined muricid and naticid incomplete drillholes on the genus followed a slightly different trend than the trend seen for muricids. The frequency of combined incomplete drillholes was higher in both the Pinecrest Beds (0.80) and the Nashua Fm. (0.441) than in the correlative Yorktownian localities, the Chowan River Fm. (0.385) and the first phase of the Waccamaw Fm. (0.353, Figure 19b). The frequency of combined incomplete drillholes on the genus was slightly lower in the Bermont Fm. (0.533) than in the second phase of the Waccamaw Fm. (0.594, Figure 19b).

Muricid and combined prey effectiveness values on *C. fornicata* were also compared for the




a.




b.

Figure 19. a., b.) Muricid (a.) and combined (b.) prey effectiveness of the genus *Crepidula* from correlative localities of the Yorktownian and Buckinghamian subprovince. Buckinghamian localities; L-Plio, Pinecrest bed 3; Plio-Pleist, Nashua Fm.; Pleist, Bermont; Yorktownian localities; L-Plio, Chowan River Fm.; Plio-Pleist, 1$^{st}$ Waccamaw; Pleist, 2$^{nd}$ Waccamaw.

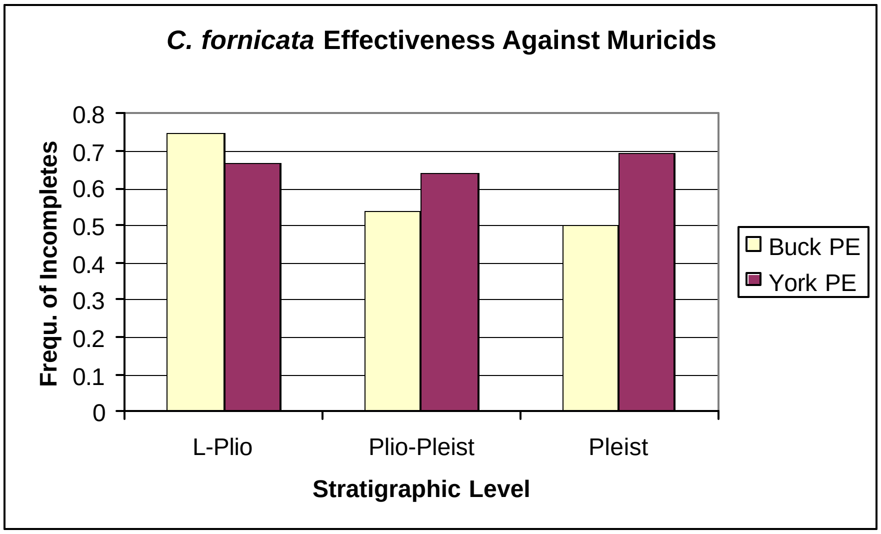
same correlative Buckinghamian and Yorktownian localities mentioned above. Muricid prey effectiveness values on *C. fornicata* followed a similar trend to that seen for the entire genus. The frequency of incomplete muricid drillholes was slightly higher in the Pinecrest Beds (0.75) than in the Chowan River Fm. (0.667, Figure 20a). Muricid prey effectiveness values on *C. fornicata* were slightly lower in the Nashua Fm. (0.536) and Bermont Fm. (0.50) than in the correlative first phase of the Waccamaw Fm. (0.643) and second phase of the Waccamaw Fm. (0.692, Figure 20a). The frequency of combined incomplete drillholes on *C. fornicata* was higher in the Pinecrest Beds (0.75) and Nashua Fm. (0.536) than in the Chowan River Fm. (0.286) and first phase of the Waccamaw Fm. (0.353, Figure 20b). Combined prey effectiveness values on *C. fornicata* were relatively lower in the Bermont Fm. (0.375) than in the second phase of the Waccamaw Fm. (0.613, Figure 20b).

Muricid and combined prey effectiveness values on *C. fornicata* and the entire genus were statistically compared using a Fisher's exact test to determine spatial variations in prey efficiency. For the most part *Crepidula* were very efficient against muricid and naticid predation in both the Buckinghamian and Yorktownian subprovinces during the Plio-Pleistocene. Although variations in prey effectiveness between these subprovinces were indicated, statistical comparisons showed no significant differences between prey effectiveness values.

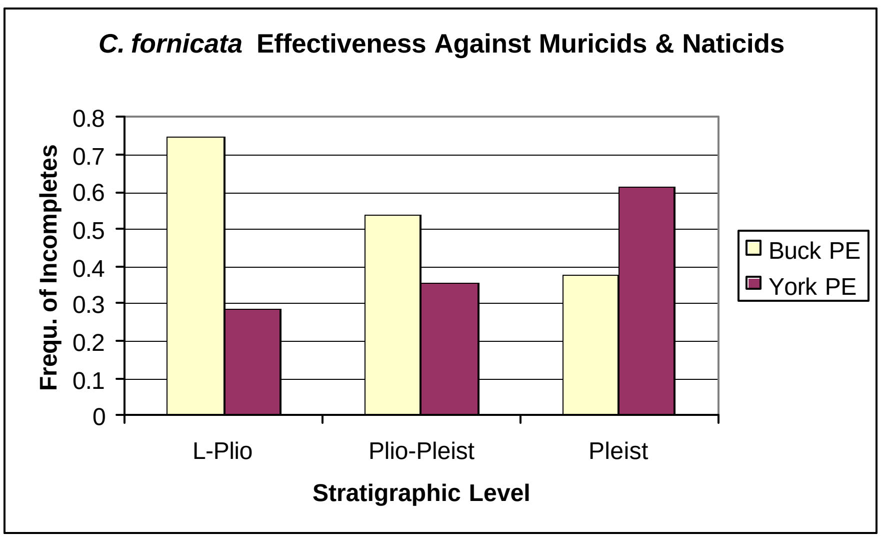
## DISCUSSION

### Temporal Variations

One of the objectives in this study was to compare predation indices from successive formations in order to determine temporal variations in muricid and naticid drilling predation of *Crepidula*. Compilations of muricid and naticid drilling frequencies on *Crepidula* from successive formations in the Yorktownian subprovince showed that combined drilling was moderate in the middle Pliocene (18.7%), gradually declined into the late Pliocene (7.5%), and increased after the Plio-Pleistocene boundary (22.2%). Temporal comparisons of drilling




a.




b.

Figure 20. a., b.) Muricid (a.) and combined (b.) prey effectiveness of the species *C. fornicata* from correlative localities of the Yorktownian and Buckinghamian subprovince. Buckinghamian localities; L-Plio, Pinecrest bed 3; Plio-Pleist, Nashua Fm.; Pleist, Bermont; Yorktownian localities; L-Plio, Chowan River Fm.; Plio-Pleist, 1st Waccamaw; Pleist, 2nd Waccamaw.

frequencies showed several cases in which there were significant differences in drilling between successive formations that appear to be associated with changes in predator behavior, prey morphology and species relative abundance, and/or environmental conditions.

Naticid drilling of *C. fornicata* was intense (20.5%) in the Rushmere Mbr. of the Yorktown Formation, and then decreased significantly to moderate levels (7.4%) in the Moore House Mbr. of the Yorktown Formation (Table 1). Naticids also exhibited selectivity with respect to species and size in the Rushmere, but did not exhibit such stereotypic behavior in the Moore House, indicating that changes in naticid behavior may have been involved in decreased drilling between these successive formations. *Crepidula aculeata* was more abundant than *C. fornicata* in the Rushmere (representing 57% and 41% of the *Crepidula* population respectively); however, naticid drilling frequencies were significantly higher for *C. fornicata* (0.205) than for *C. aculeata* (0.049). Size frequency distributions of *C. fornicata* in the Rushmere showed that 36% of the specimens were 25-35mm in size and 39% of the specimens were 35-45mm in size; however there was a significant difference in the percentage of drilled specimens between these size classes. Naticids drilled approximately 41% of individuals ranging from 35-45mm in size, but none of the specimens ranging from 25-35mm in size were drilled by naticids. Naticid drilling and selectivity of *C. fornicata* decreased in the Moore House, despite the fact that *C. fornicata* became more abundant; however, *C. fornicata* specimens in the Moore House are generally smaller than in the Rushmere, with most individuals bearing shells 15-25mm in size. Naticid selectivity of *C. fornicata* appears to be influenced by the size distribution of individuals present rather than the abundance of the species. Therefore, decreased naticid drilling of *C. fornicata* between the Rushmere and Moore House is most likely due to individuals decreasing in size rather than a decrease in naticid selectivity, and reduced size of *C. fornicata* may be due to a preservational bias for smaller specimens.

Temporal comparisons of *Crepidula* from the first phase of the Waccamaw Fm. and the James City Fm. showed differences in species diversity, predation intensity, and prey effectiveness.

*Crepidula* were more diverse in the James City (3 species present) than in the Waccamaw (1 species present). Muricid drilling of *Crepidula* was low (3.6%) in the first phase of the Waccamaw Formation and increased significantly (15%) in the James City Formation. Muricids also exhibited selectivity with respect to prey species and size in the James City, but lacked such stereotypic behavior in the Waccamaw. The most abundant *Crepidula* species in the James City was *C. aculeata* (representing 67% of the *Crepidula* population), and *C. fornicata* was the second most abundant species (representing 29% of the population). Most specimens of *C. fornicata* in the James City were medium-sized, bearing shells 25-35mm (51% of individuals) and 35-45mm (30% of individuals) in length. Muricids showed a preference for larger individuals, drilling 44% of those measuring 35-45mm, in comparison to only 15% of those measuring 25-35mm. Increases in drilling frequencies and species diversity of *Crepidula* in the James City also supports the hypothesis that intense predation increases species diversity within communities by preventing the utilization of resources by a dominant species (Paine, 1966, 1981; Hansen and Kelley, 1995).

Muricids were not selective of *Crepidula* in the Waccamaw, possibly due to the fact that the *Crepidula* population was completely dominated by *C. fornicata,* most of which were 35-45mm in length. The frequency of incomplete muricid drillholes was significantly higher in the Waccamaw (0.643) than in the James City (0.276), most likely due to *C. fornicata* bearing larger shells in the Waccamaw than in the James City (Table 8). Differences in shell size and relative abundance of *C. fornicata* in the Waccamaw and James City was probably caused by environmental change.

The Waccamaw possessed some characteristics of a subtropical environment in that it was warm, very productive, and contained a variety of subtropical molluscan species. In contrast, the James City was cooler and less productive than the Waccamaw, and there was no subtropical influence in the James City. Warm water in the Waccamaw enhanced the precipitation of calcium carbonate, thus allowing *Crepidula* to increase in size. Environmental cooling and decreased productivity in the James City may have caused *C. fornicata* to decrease in size and abundance. Those individuals of *C. fornicata* in the James City that did grow to be 35-45mm in size were much thinner than individuals that size in the Waccamaw, increasing the likelihood of successful predation. Therefore, significant differences in prey effectiveness and predation intensity between the Waccamaw and James City may have been influenced by environmental changes that occurred between these successive formations. Furthermore, increased predation intensity in the James City may have played a significant role in *Crepidula* becoming more diverse.

Temporal trends in predation intensity and prey effectiveness may also have been influenced by changes in predator diversity. Predation intensity decreased through the Pliocene, and combined drilling frequencies were lowest (0.075) in the Chowan River Formation. The muricid genus *Ecphora* was a dominant drilling predator throughout the Miocene and most of the Pliocene, and this genus went extinct between the Moore House and Chowan River Formation. Decreased drilling could have been due, in part, to the extinction of this genus. Significant differences in combined drilling frequencies and prey effectiveness values between the first phase of the Waccamaw and James City Formation may have been influenced by the disappearance of the muricid genera *Chicoreus* and *Phyllonotus* between these formations. These two subtropical genera were fairly abundant in the Waccamaw, but cooler conditions in the James City forced these predators to lower latitudes. Competition among predators was intense during the Waccamaw, and both *Chicoreus* and *Phyllonotus* probably had to compete for the same individual on occasion. Group foraging has been observed in recent laboratory experiments by Dietl (pers. comm.) in both of these muricid groups. Recent observations of group foraging by the species, *Chicoreus dilectus,* resulted in one complete and three incomplete drillholes on a single individual of the prey species *Chione elevata* (Figure 21a, b). This observation suggests that high prey effectiveness in the Waccamaw may be exaggerated due to the occurrence of incomplete and complete drillholes on the same prey specimen. Prey effectiveness measures the

a. 

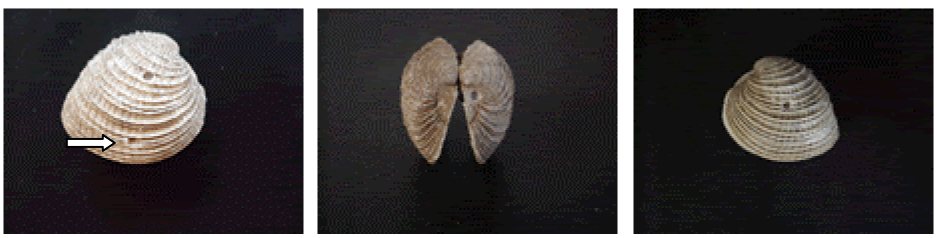
b. 

Figure 21. a., b.) a.) Laboratory observation of three individuals of *Chicoreus dilectus* drilling one individual *Chione elevata.* b.) Same *Chione* specimen from different viewpoints showing three incomplete drillholes and one complete drillhole. Complete drillhole indicated with the white arrow. Laboratory observations and photographs courtesy of Dr. Greg P. Dietl.

frequency of incomplete drillholes out of the total number of attempted drillholes and is used as a proxy for unsuccessful predation. Group foraging could result in a successfully attacked individual with incomplete drillholes that did not contribute to the evolution of the species. There were a lot of individuals in the Waccamaw with multiple drillholes; however, after checking over the data from this locality there were no cases of incomplete and complete drillholes occurring on a single specimen.

Spatial Variations

The second objective in this study was to compare predation indices from three formations in Virginia and North Carolina to three correlative formations in Florida in order to determine how drilling predation on *Crepidula* is influenced by environmental variables associated with two distinct geographic areas. Comparing differences in faunal diversity and predation indices between these correlative formations revealed latitudinal trends in predation intensity that appear to be influenced by geographic variations in predator diversity and *Crepidula* species diversity.

The diversity of predatory gastropods increases towards the equator (Marincovich, 1977; Taylor and Taylor, 1977). Predators and predation intensity have been shown to increase species diversity within a population by preventing resources from being utilized by a dominant species (Paine, 1966). After closely observing molluscan faunas from each locality, it was determined that predators were more diverse in Florida than in North Carolina and Virginia, especially for muricids. *Crepidula* were more diverse in Florida in two of the formations, and were slightly less diverse in the other formation. This result is in accord with observations of an equatorward increase in the diversity of drilling gastropods (Taylor and Taylor, 1977), and also supports the notion that predators increase species diversity (Paine, 1966, 1981).

Spatial comparisons of predation intensity showed that drilling frequencies on *Crepidula* were much higher in North Carolina and Virginia than in Florida. Statistical comparisons revealed that drilling was significantly higher in both phases of the Waccamaw Formation than in the Nashua and Bermont formations, and in both of these localities the *Crepidula* population was dominated by a single species.  This result contradicts the view that predation intensity increases species diversity by preventing resources from being utilized by a dominant species.  A latitudinal increase in drilling was also reported for modern bivalves (Vermeij et al., 1989), Paleocene turritellids (Allmon et al., 1990), and Eocene molluscan faunas (Hansen and Kelley, 1995).  An equatorward decrease in drilling contradicts the view that, due to an increase in diversity, predators have a greater ecological impact in tropical environments than in temperate environments (Vermeij, 1987; Taylor and Taylor, 1977; Marincovich, 1977; Vermeij and Dudley, 1982).  However, predator diversity and species diversity increases towards the equator, which causes competition between predator species to be more intense.  Intense competition is a risk to drilling predators; competition increases the chances of drilling being interrupted because this method of predation is a time consuming process.  Therefore, higher drilling frequencies in North Carolina and Virginia than in Florida were probably due, in part, to competition among predators being less intense at higher latitudes, which allowed predators a sufficient amount of time to drill their prey successfully.

Pliocene vs. Pleistocene

The third objective to this study was to compare variations in predation indices and species relative abundances of *Crepidula* populations in the late Pliocene and early Pleistocene in order to determine if the Plio-Pleistocene extinction event affected the tempo and mode of evolution within the genus *Crepidula*.  Differences in species relative abundances of *Crepidula* and muricid and naticid predation indices on *Crepidula* between Plio-Pleistocene formations in Florida and in North Carolina and Virginia appear to be correlated with environmental changes caused by the Plio-Pleistocene extinction event.

Comparisons of *Crepidula* species from pre- and post-extinction faunas in North Carolina and in Florida revealed that *C. fornicata* decreased in abundance and *C. aculeata* increased in abundance in both areas.  The *Crepidula* population in the first phase of the Waccamaw Fm. was completely dominated by *C. fornicata* (100% of population), but drastically decreased in abundance in the James City Fm. (29% of population). *Crepidula aculeata* was not present in the Waccamaw, but was the most abundant *Crepidula* species in the James City (67% of population), replacing *C. fornicata* as the dominant species in this *Crepidula* population (Table 14). The *Crepidula* population in the Nashua Fm. was dominated by *C. fornicata* (66% of population), and *C. aculeata* was not present in this population. *Crepidula fornicata* decreased in abundance in the Bermont Fm. (8% of population), and *C. aculeata* was the most abundant species in the Bermont (34% of population), replacing *C. fornicata* as the dominant species in this *Crepidula* population (Table 15). Climatic cooling occurring between the Waccamaw and James City formations, and the Nashua and Bermont formations, resulted in the depletion of *C. fornicata*. *Crepidula aculeata* was absent from the pre-extinction faunas, and then was the dominant *Crepidula* species in the post-extinction faunas, suggesting that *C. aculeata* possibly filled the niche space that was left open with the depletion of *C. fornicata*.

Differences in muricid and naticid drilling frequencies and prey effectiveness values on *Crepidula* from pre- and post-extinction faunas indicate that environmental changes associated with the Plio-Pleistocene extinction could have also affected predation patterns on *Crepidula*. Muricid and combined drilling frequencies on *C. fornicata* significantly increased (from 3.6% and 14.5% to 24.5% and 39.6%) between the first phase of the Waccamaw Fm. and the James City Formation (Table 3), and muricid prey effectiveness values significantly decreased (from 0.643 and 0.353 to 0.276 and 0.216) between these two formations (Table 9). The environment in the James City was cooler and less productive than in the Waccamaw, causing *C. fornicata* to decrease in size and abundance. Specimens in the James City also appear thinner than those in the Waccamaw, and reduced shell thickness of *C. fornicata* in the James City would decrease the amount of time it takes a predator to successfully drill its prey, therefore increasing the frequency of complete drillholes and decreasing the frequency of incomplete drillholes. Reduced temperatures and productivity in the James City resulted in *C. fornicata* losing adaptations that helped in resisting predators in the Waccamaw. This result was similar to studies that showed decreasing temperatures and productivity caused hard-bottom gastropods possessing anti-predatory characteristics to be drastically reduced, or go extinct; species lacking such anti-predatory adaptations were not as severely impacted by the environmental changes (Vermeij and Petuch, 1986; Vermeij, 1987).

Comparisons of muricid and naticid drilling frequencies and prey effectiveness values on *C. fornicata* from the Nashua and Bermont formations revealed a trend similar to that seen in North Carolina. Drilling frequencies on *C. fornicata* increased (from 8.7% and 0.7% to 13.0% and 8.7%) between the Nashua and Bermont, and prey effectiveness values decreased (from 0.536 to 0.375) between these formations; however, differences were not statistically significant. Therefore, it appears that predation of *C. fornicata* in Florida was not as affected by the Plio-Pleistocene extinction as it was in North Carolina; however, similar patterns with respect to the relative abundances of *C. fornicata* and *C. aculeata* and predation indices on *C. fornicata* in both areas provide at least some evidence to suggest that the Plio-Pleistocene extinction impacted the evolution of *C. fornicata* and *C. aculeata*.

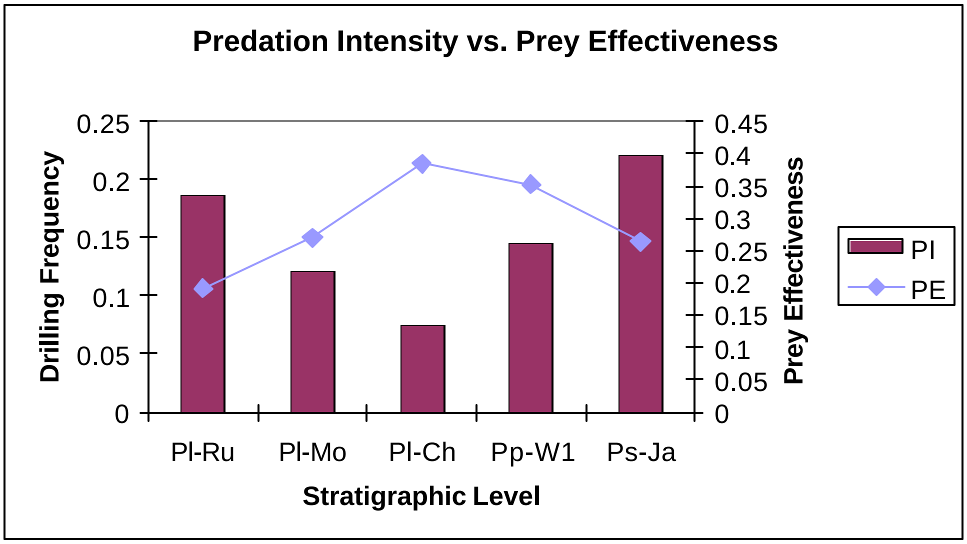
Comparisons of muricid drilling frequencies on the genus *Crepidula* from pre- and post-extinction faunas in Florida revealed a trend opposite to the trend in North Carolina. Muricid drilling of *Crepidula* significantly decreased, rather than increased, in Florida following the Plio-Pleistocene extinction. Muricids exhibited selectivity with respect to drillhole site on the prey's shell in the Pliocene of Florida, but were not site selective in the Pleistocene of Florida. The loss of such stereotyped behavior in muricids probably contributed to decreased drilling by muricids after the extinction. Naticids did not exhibit selectivity of drillhole site in the Pliocene, but were site selective in the Pleistocene, and, as a result, naticid drilling frequencies on the genus *Crepidula* increased significantly (from 1.0% to 4.0%) following the extinction. *Crepidula* increased in size and species diversity between the Nashua (12.7mm avg. length, 3 species present) and Bermont (22.9 avg. length, 5 species present) formations, and most individuals were singly attached to a substrate. Solitary life habit and size increase of *Crepidula* favors naticids because they are generally larger than muricids, thus preferring larger prey, and their method of feeding is better suited for solitary individuals, as opposed to stacked individuals, because it is easier for naticids to secure one individual than a stack of individuals.

Evolutionary Implications

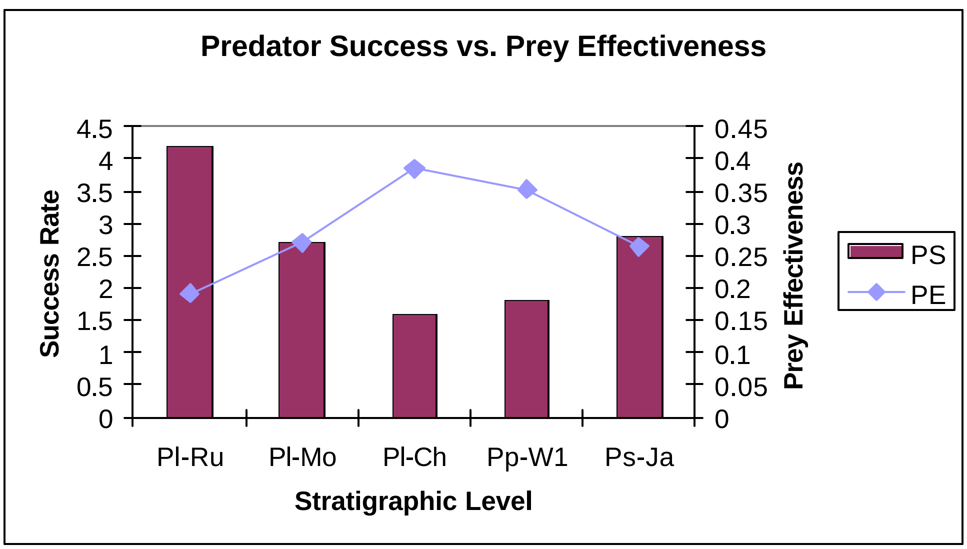
The fourth, and final, objective to this study was to determine if predator-prey interaction between drilling muricid and naticid gastropods and prey species within the gastropod genus *Crepidula* provides evidence for escalation and/or coevolution. Comparisons of successful and unsuccessful drilling predation on *Crepidula* from successive formations revealed opposing trends in predation intensity and prey effectiveness (Figure 22a), which does not support coevolution because predator and prey are not reciprocally responding to one another. Temporal and spatial variations in combined muricid and naticid drilling frequencies and prey effectiveness on *Crepidula* indicated that predator-prey interaction of this particular system appears to be influenced by changes in competition, providing some evidence for escalation.

Prey effectiveness measures the percentage of attempted drillholes that were incomplete, and represents the proportion of predatory attacks that were unsuccessful. Rates of successful predation were determined by dividing the total number of complete drillholes by the total number of incomplete drillholes. Rates of successful predation and prey effectiveness on *Crepidula* from successive formations were statistically compared using a correlation coefficient (= -0.8), and differences were inversely correlated and statistically significant ($p < 0.05$, Figure 22b). Predation success rates were used instead of drilling frequencies because they involve only those individuals that were subjected to drilling predation. Individuals that were not drilled were eliminated because they are unable to respond evolutionarily to drilling predation if they were not selected as possible prey by predators.

Temporal trends in predator success rates were similar to trends in predation intensity. Rates of successful predation decreased gradually through the Pliocene, and then increased significantly in the Pleistocene. In contrast, prey effectiveness increased gradually through the Pliocene, and




a.




b.

Figure 22. a., b.) a.) Combined muricid and naticid drilling frequencies (PI) and prey effectiveness (PE) on *Crepidula* from successive Yorktownian formations. b.) Muricid and naticid predator success rate (PS) and prey effectiveness (PE) on *Crepidula* from successive Yorktownian formations. Abbreviations for stratigraphic levels are the same as in Figure 7.

decreased significantly in the Pleistocene. Differences in predation intensity, prey effectiveness, and predator success rates between successive formations are correlated with decreases in predator competition and diversity, suggesting that extremely high frequencies of incomplete drillholes on *Crepidula* in the first phase of the Waccamaw Fm. were possibly due to drilling being interrupted by predators competing for the same prey, and/or predators being interrupted by their own enemies. Significantly higher frequencies of complete drillholes in the James City Fm. were likely due to the absence of several lineages of subtropical muricid gastropods, which caused competition between predators to decrease, and decreased the chances of drilling being interrupted.

Escalation involves the accumulation of adaptations of the prey in response to their enemies, and the pace at which it occurs depends on the ability of a species to adapt to changes in competition, predation, and environmental conditions (Vermeij, 1987; Kelley and Hansen, 2001). Escalation predicts that competition and predation have increased through time, and the survival of a lineage depends on whether or not its individuals adapt to these increasing biological hazards, which is often achieved through behavioral and/or morphological changes. Predator diversity and competition appear to play a major role in predator-prey interaction between muricid and naticid gastropods and the gastropod genus *Crepidula*. High diversity and intense competition between gastropod predators seems to give *Crepidula* an advantage against drilling predators, but this genus has been able to adapt in times when competition is low and predation is intense. Unlike most molluscan lineages, which adapt through behavioral or morphologic change, *Crepidula* may change morphologically, but are more likely adapting to this increased threat of predation by utilizing a specialized mode of reproduction that ensures a sufficient number of individuals reach sexual maturity. Most *Crepidula* species can also tolerate numerous environments, thus allowing possible escape from predators by migrating to environments not suited for their enemies. Escalation was supported in this study because even though predation intensity decreased in the Pliocene, it does not appear to be due to decreased efficiency of the predator, but rather due to the intensification of predator competition becoming an increased threat to the predators themselves. When competition decreases, predation intensity on *Crepidula* increases, but the *Crepidula* have been able to adapt to their enemies utilizing life habit and reproductive strategies that are advantageous in surviving changes in both the biological and physical hazards of the environment.

## CONCLUSION

There is evidence in this study to suggest that temporal trends in muricid and naticid drilling predation on *Crepidula* were influenced by changes in predator behavior, prey morphology, prey diversity, and prey size. These changes tend to be correlated with changes in the physical environment, and do not appear to be the result of biological interaction acting alone. However, there is some indication that variations in drilling predation are correlated with changes in predator competition, suggesting that competition is a forcing mechanism driving such trends, and also indicating the importance of biologic interaction in evolution.

Spatial trends in muricid and naticid drilling predation on *Crepidula* were also influenced by predator diversity and competition. There was an inverse relationship between predation intensity and predator diversity and competition. A latitudinal increase in predation intensity was most likely due to diversity and competition decreasing with latitude because drilling is less likely to be interrupted when competition among predators is low.

Significant differences in muricid and naticid predation intensity and prey effectiveness on *Crepidula* from pre- and post-extinction faunas appear to be influenced by environmental change as well as changes in predator diversity. The subtropical influence in the pre-extinction fauna was lost due to climatic cooling. All of the subtropical gastropod predators were absent in the post-extinction fauna, resulting in less competition between predators. *Crepidula fornicata* was the dominant species before the extinction in both the temperate and subtropical localities. *Crepidula fornicata* decreased in size and abundance following the extinction, and *C. aculeata* replaced *C. fornicata* as the dominant species in both localities. Predator-prey interaction of this system once again appears to be influenced by competition across the Plio-Pleistocene extinction boundary; however, changes in competition were caused by environmental differences between the pre- and post-extinction faunas.

This study showed that competition among predators has played an important role in the evolution of this particular predator-prey system. Competition levels appear to be a dominant factor in determining the pace and direction of temporal and spatial trends in drilling predation of *Crepidula*. Life history strategies of the genus *Crepidula* have helped this lineage succeed in adapting to temporal increases in the biological hazards of evolution. This study provided evidence for an increase in biological hazards through time, as well as evidence of organisms adapting to such hazards, thus supporting escalation and the importance of biological interaction in evolution.

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APPENDIX

Appendix A. Data tabulation from each locality in this study. (Abbreviations listed on p. 122.)

| **Strat. Interval** | **Species** | **L** | **H** | **W** | **CD** | **ID** | **Dr. Loc.** | **Dr. Type** |
|---|---|---|---|---|---|---|---|---|
| Raysor Fm. | *C. aculeata* | 29.6 | 11.0 | 25.9 | | | | |
| Goose Creek, SC | | 35.7 | 13.3 | 32.1 | 1 | | 3 | nat |
| | | 27.7 | 8.7 | 22.7 | 1 | | 3 | nat |
| | | 38.2 | 14.6 | 31.8 | 2 | 1 | cd-3,4; id-4 | all mur |
| | | 27.0 | 10.0 | 20.4 | | | | |
| | | 29.6 | 9.6 | 26.7 | 1 | | 3 | nat |
| | | 36.3 | 13.8 | 35.2 | | | | |
| | | 25.5 | 12.5 | 21.3 | | | | |
| | | 29.0 | 11.2 | 21.6 | | | | |
| | | 12.0 | 5.0 | 8.7 | | | | |
| | | 24.2 | 11.1 | 17.6 | | | | |
| | | 27.3 | 7.8 | 21.0 | | | | |
| | | 25.8 | 8.1 | 21.1 | | | | |
| | | 19.4 | 6.6 | 14.7 | | | | |
| | | 17.7 | 6.6 | 14.1 | | | | |
| | | 24.3 | 7.8 | 18.6 | | | | |
| | | 15.2 | 4.1 | 12.8 | | | | |
| | | 18.7 | 7.4 | 14.3 | | | | |
| | | 20.8 | 8.6 | 15.5 | 1 | | 3 | nat |
| | | 24.8 | 6.7 | 19.9 | | | | |
| | | 9.9 | 3.7 | 8.3 | | | | |
| | | 33.2 | 12.3 | 24.1 | | | | |
| | | **25.1** | **9.1** | **20.4** | | | | |
| | | | | | | | | |
| | *C. fornicata* | 28.3 | 6.4 | 21.5 | | | | |
| | | 27.0 | 6.6 | 20.7 | | | | |
| | | 12.0 | 3.6 | 8.3 | | | | |
| | | 17.1 | 5.8 | 15.3 | | | | |
| | | 48.7 | 19.0 | 33.8 | | | | |
| | | 41.9 | 18.0 | 21.8 | 1 | | 2 | nat |
| | | 18.3 | 6.8 | 12.8 | 1 | | 1 | nat |
| | | 26.2 | 9.9 | 17.4 | | | | |
| | | 37.0 | 12.3 | 31.0 | | | | |
| | | 18.1 | 7.9 | 15.0 | | | | |
| | | 36.9 | 12.7 | 28.6 | | | | |
| | | 34.7 | 12.4 | 25.0 | | | | |
| | | 44.3 | 15.3 | 25.6 | | | | |
| | | 37.6 | 16.4 | 29.1 | | | | |
| | | 30.5 | 9.6 | 22.2 | | | | |
| | | 34.4 | 13.7 | 23.4 | | | | |
| | | 50.3 | 15.8 | 32.3 | 2 | | 1,4 | mur |
| | | 36.9 | 8.4 | 25.2 | | | | |

| **Strat. Interval** | **Species** | **L** | **H** | **W** | **CD** | **ID** | **Dr. Loc.** | **Dr. Type** |
|---|---|---|---|---|---|---|---|---|
| Raysor Fm. | *C. fornicata* | 42.1 | 12.9 | 29.0 | | 1 | 3 | mur |
| Goose Creek, SC | | 13.1 | 3.5 | 8.5 | | | | |
| | | 9.0 | 3.8 | 6.6 | | | | |
| | | 39.2 | 15.4 | 23.4 | | | | |
| | | 24.3 | 10.7 | 16.4 | | | | |
| | | 24.0 | 12.7 | 16.0 | | | | |
| | | 40.0 | 15.6 | 20.3 | | | | |
| | | 26.9 | 11.6 | 14.8 | | | | |
| | | 34.3 | 12.2 | 24.8 | 1 | | 4 | nat |
| | | 40.7 | 14.9 | 24.0 | | | | |
| | | 41.4 | 15.6 | 19.2 | | | | |
| | | 36.0 | 16.7 | 21.0 | | | | |
| | | 35.7 | 14.7 | 25.3 | 1 | | 3 | nat |
| | | 28.1 | 13.4 | 16.9 | | | | |
| | | 26.2 | 11.5 | 21.1 | | | | |
| | | 28.7 | 12.4 | 20.5 | | | | |
| | | 36.8 | 15.2 | 23.4 | | | | |
| | | 22.0 | 12.5 | 16.1 | | | | |
| | | 37.8 | 14.0 | 23.7 | | | | |
| | | 32.6 | 13.6 | 19.5 | | | | |
| | | 39.4 | 16.5 | 18.4 | 1 | | 5 | mur |
| | | 29.1 | 10.5 | 19.1 | | | | |
| | | 25.3 | 10.2 | 16.1 | | | | |
| | | 36.3 | 14.7 | 21.2 | | 2 | 4,5 | mur |
| | | 33.9 | 15.7 | 17.9 | | | | |
| | | 33.1 | 14.2 | 20.4 | | | | |
| | | 32.3 | 14.6 | 20.5 | | 1 | 3 | mur |
| | | **31.7** | **12.2** | **20.7** | | | | |
| | | | | | | | | |
| | *C. convexa* | 53.5 | 16.6 | 33.7 | | 1 | 1 | mur |
| | | 22.3 | 8.5 | 17.1 | | | | |
| | | 16.6 | 5.4 | 10.3 | | | | |
| | | 12.0 | 3.2 | 9.0 | | | | |
| | | 12.2 | 4.1 | 8.2 | | | | |
| | | 12.1 | 4.3 | 7.4 | | | | |
| | | 11.8 | 4.2 | 8.6 | | | | |
| | | 13.5 | 5.0 | 9.1 | | | | |
| | | 12.2 | 4.1 | 8.9 | | | | |
| | | 13.7 | 4.1 | 10.4 | 1 | | 4 | mur |
| | | 23.4 | 10.6 | 16.1 | | | | |
| | | 20.5 | 8.0 | 13.2 | | | | |
| | | 20.7 | 9.2 | 16.7 | | | | |
| | | 20.2 | 7.5 | 12.8 | | | | |
| | | 17.9 | 8.0 | 12.0 | | | | |
| | | 40.7 | 15.8 | 26.3 | | | | |
| | | 11.0 | 5.0 | 5.7 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Raysor Fm. | *C. convexa* | 19.1 | 7.2 | 12.7 | 1 | | 2 | mur |
| Goose Creek, SC | | 11.5 | 4.4 | 6.2 | | | | |
| | | 42.7 | 17.6 | 29.9 | | | | |
| | | 48.0 | 17.2 | 26.7 | | | | |
| | | 45.1 | 16.4 | 27.4 | | | | |
| | | 47.1 | 14.6 | 27.1 | | | | |
| | | 28.0 | 14.3 | 20.3 | | | | |
| | | **24.0** | **9.0** | **15.7** | | | | |
| | | | | | | | | |
| | *C. plana* | 11.1 | 1.2 | 8.1 | | | | |
| | | 7.2 | 1.0 | 5.8 | | | | |
| | | 32.1 | 4.7 | 22.1 | | | | |
| | | **16.8** | **2.3** | **12.0** | | | | |
| | | | | | | | | |
| Duplin Fm. | *C. convexa* | 12.0 | 5.6 | 7.9 | | | | |
| Lumberton, NC | | 10.3 | 4.5 | 6.2 | | | | |
| | | 7.4 | 2.4 | 5.1 | | | | |
| | | 10.3 | 4.6 | 5.7 | | | | |
| | | 10.8 | 4.2 | 6.7 | | | | |
| | | 31.9 | 13.5 | 21.3 | | | | |
| | | 10.6 | 5.2 | 5.5 | | | | |
| | | 8.4 | 3.7 | 4.8 | | | | |
| | | 16.9 | 4.8 | 11.1 | | | | |
| | | 18.6 | 5.2 | 11.6 | 1 | | 1 | mur |
| | | 9.9 | 4.2 | 5.2 | | | | |
| | | 9.7 | 4.5 | 5.2 | | | | |
| | | **13.1** | **5.2** | **8.0** | | | | |
| | | | | | | | | |
| | *C. fornicata* | 30.0 | 9.8 | 24.8 | | | | |
| | | 25.9 | 5.8 | 16.3 | | | | |
| | | 12.2 | 3.6 | 8.9 | | | | |
| | | 11.4 | 2.4 | 7.8 | | | | |
| | | 13.9 | 5.9 | 9.7 | 1 | | 3 | nat |
| | | 21.9 | 7.1 | 15.5 | | | | |
| | | 14.7 | 4.3 | 10.7 | | | | |
| | | 28.0 | 6.6 | 21.2 | | | | |
| | | 21.2 | 7.0 | 15.9 | | | | |
| | | 11.2 | 4.0 | 7.5 | | | | |
| | | 34.3 | 15.8 | 26.3 | | | | |
| | | 25.5 | 12.8 | 17.6 | | | | |
| | | 31.1 | 8.7 | 20.6 | | | | |
| | | 17.1 | 7.8 | 13.2 | | | | |
| | | 21.3 | 6.8 | 13.6 | | | | |
| | | 29.6 | 10.5 | 21.4 | | | | |
| | | 34.0 | 16.4 | 24.8 | | | | |
| | | 24.8 | 12.6 | 18.1 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Duplin Fm. | *C. fornicata* | 28.2 | 11.5 | 20.7 | 1 | | 3 | mur |
| Lumberton, NC | | 36.2 | 18.0 | 25.1 | | | | |
| | | 36.4 | 18.2 | 24.6 | | | | |
| | | 30.5 | 13.0 | 23.5 | 1 | | 3 | mur |
| | | 29.0 | 15.1 | 21.2 | | | | |
| | | 35.3 | 14.8 | 24.6 | | | | |
| | | 31.1 | 11.7 | 20.9 | | | | |
| | | 33.9 | 13.3 | 25.8 | | | | |
| | | 39.3 | 16.8 | 29.3 | | 1 | 1 | nat |
| | | 33.7 | 16.7 | 24.2 | | | | |
| | | 23.4 | 10.1 | 18.7 | | 1 | 1 | mur |
| | | 30.1 | 10.7 | 21.5 | | | | |
| | | 17.5 | 4.9 | 12.5 | | | | |
| | | 35.0 | 10.5 | 31.0 | | | | |
| | | 20.8 | 4.8 | 16.6 | | | | |
| | | 29.1 | 6.5 | 20.9 | | | | |
| | | 24.1 | 5.0 | 18.0 | | | | |
| | | 24.8 | 6.9 | 18.4 | | | | |
| | | 34.5 | 8.8 | 26.7 | | | | |
| | | 42.5 | 12.2 | 32.3 | 1 | | 3 | nat |
| | | 30.8 | 9.4 | 22.3 | | | | |
| | | 35.3 | 6.6 | 27.6 | | | | |
| | | 35.6 | 9.4 | 26.5 | | | | |
| | | 41.7 | 8.2 | 38.0 | | | | |
| | | 7.9 | 2.2 | 5.5 | | | | |
| | | 21.2 | 4.9 | 15.8 | | 1 | 1 | mur |
| | | 25.6 | 4.7 | 16.8 | | | | |
| | | 12.8 | 3.1 | 8.8 | | | | |
| | | 26.0 | 5.3 | 18.8 | | | | |
| | | 30.0 | 6.1 | 22.8 | | | | |
| | | 12.0 | 2.3 | 9.8 | | | | |
| | | 22.7 | 7.6 | 17.4 | | 1 | 1 | mur |
| | | 43.7 | 9.2 | 32.8 | | 1 | 3 | mur |
| | | 33.3 | 8.4 | 27.1 | | | | |
| | | 37.7 | 8.2 | 29.1 | | | | |
| | | 22.9 | 5.1 | 16.4 | | | | |
| | | 28.1 | 11.0 | 23.4 | | | | |
| | | 32.7 | 10.4 | 26.1 | 1 | | 3 | mur |
| | | 44.6 | 17.1 | 32.8 | | | | |
| | | 36.2 | 13.5 | 27.8 | 1 | | 3 | mur |
| | | 20.4 | 5.1 | 14.1 | | | | |
| | | 24.6 | 6.9 | 19.2 | | | | |
| | | 21.6 | 7.2 | 15.4 | 1 | | 3 | mur |
| | | 20.1 | 8.1 | 16.2 | 3 | | 3,4,5 | all mur |
| | | 13.9 | 4.9 | 9.8 | | | | |
| | | 10.7 | 3.1 | 7.6 | | | | |

| **Strat. Interval** | **Species** | **L** | **H** | **W** | **CD** | **ID** | **Dr. Loc.** | **Dr. Type** |
|---|---|---|---|---|---|---|---|---|
| Duplin Fm. | *C. fornicata* | 10.5 | 2.7 | 5.9 | 1 | | 3 | mur |
| Lumberton, NC | | 9.7 | 2.8 | 7.2 | | | | |
| | | **26.3** | **8.7** | **19.6** | | | | |
| | | | | | | | | |
| Duplin Fm. | *C. plana* | 34.2 | 5.5 | 22.9 | | | | |
| Lumberton, NC | | 35.3 | 7.6 | 20.5 | | | | |
| | | 30.0 | 5.2 | 19.7 | | | | |
| | | 16.4 | 2.9 | 11.2 | | | | |
| | | 28.9 | 6.4 | 20.8 | | | | |
| | | 29.0 | 6.6 | 24.8 | | | | |
| | | 29.0 | 4.2 | 17.6 | | | | |
| | | 27.2 | 4.0 | 18.0 | | | | |
| | | 29.9 | 3.4 | 21.6 | | | | |
| | | 26.2 | 3.4 | 17.0 | | | | |
| | | 13.0 | 2.7 | 8.9 | 1 | | 3 | nat |
| | | 32.3 | 7.4 | 24.2 | | | | |
| | | 23.4 | 6.1 | 16.5 | | | | |
| | | 32.5 | 7.4 | 23.8 | | | | |
| | | 31.7 | 6.7 | 25.6 | | | | |
| | | 38.9 | 7.6 | 22.4 | | | | |
| | | 29.3 | 4.7 | 21.2 | | | | |
| | | 22.3 | 3.6 | 16.6 | | | | |
| | | 25.6 | 4.5 | 17.7 | | | | |
| | | 29.4 | 4.0 | 21.5 | | | | |
| | | 33.9 | 4.1 | 24.8 | | | | |
| | | 22.8 | 3.6 | 18.2 | | | | |
| | | 25.4 | 2.8 | 15.9 | | | | |
| | | **28.1** | **5.0** | **19.6** | | | | |
| | | | | | | | | |
| Rushmere Mbr. | *C. fornicata* | 39.9 | 14.0 | 29.5 | | | | |
| Lt. Run, VA | | 21.6 | 5.2 | 14.7 | | | | |
| | | 28.7 | 6.9 | 21.9 | | 1 | 3 | mur |
| | | 26.0 | 11.6 | 20.8 | 1 | | 1 | mur |
| | | 27.4 | 10.8 | 20.3 | | | | |
| | | 38.3 | 11.7 | 24.0 | 1 | | 3 | nat |
| | | 24.2 | 6.7 | 18.3 | | | | |
| | | 23.3 | 8.2 | 18.9 | | | | |
| | | 22.0 | 6.5 | 16.7 | 1 | | 3 | nat |
| | | 35.2 | 13.5 | 23.9 | 1 | | 4 | nat |
| | | 29.5 | 11.3 | 17.6 | | | | |
| | | 33.3 | 9.0 | 27.5 | | | | |
| | | 32.8 | 11.8 | 24.4 | | | | |
| | | 50.1 | 17.3 | 41.2 | | 1 | 4 | mur |
| | | 27.3 | 6.5 | 22.3 | | | | |
| | | 41.5 | 11.6 | 30.8 | 1 | 2 | cd-4, id-1,3 | cd-nat, id-mur |
| | | 46.3 | 13.8 | 32.6 | 1 | | 1 | mur |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Rushmere Mbr. | *C. fornicata* | 36.7 | 14.3 | 24.6 | | | | |
| Lt. Run, VA | | 39.6 | 15.2 | 26.2 | | | | |
| | | 37.9 | 13.1 | 26.8 | 1 | | 3 | nat |
| | | 35.4 | 17.4 | 25.7 | | | | |
| | | 41.5 | 14.7 | 31.5 | | | | |
| | | 30.6 | 9.4 | 24.6 | | | | |
| | | 27.7 | 8.6 | 21.3 | | | | |
| | | 34.9 | 15.2 | 25.7 | | | | |
| | | 39.7 | 8.6 | 20.0 | 1 | | 3 | nat |
| | | 48.2 | 14.2 | 35.6 | | | | |
| | | 37.6 | 12.4 | 28.1 | | | | |
| | | 36.5 | 14.1 | 24.1 | 1 | | 3 | nat |
| | | 34.1 | 11.2 | 26.0 | | | | |
| | | 37.2 | 13.2 | 29.3 | | | | |
| | | 30.6 | 9.0 | 21.3 | | | | |
| | | 31.2 | 7.8 | 24.4 | 1 | | 2 | mur |
| | | 29.2 | 7.5 | 22.5 | | | | |
| | | 20.9 | 6.4 | 15.6 | | | | |
| | | 30.7 | 8.6 | 20.0 | | | | |
| | | 38.2 | 10.9 | 32.1 | | | | |
| | | 30.5 | 10.1 | 20.5 | | | | |
| | | 14.6 | 4.2 | 10.9 | | | | |
| | | 42.1 | 19.5 | 26.8 | 1 | | 2 | nat |
| | | 37.5 | 14.8 | 22.7 | | | | |
| | | 22.8 | 8.4 | 17.2 | | | | |
| | | 23.9 | 8.3 | 17.9 | 1 | | 3 | nat |
| | | 42.5 | 20.7 | 23.7 | | | | |
| | | **33.2** | **11.2** | **23.9** | | | | |
| | | | | | | | | |
| | *C. aculeata* | 44.3 | 15.8 | 29.8 | | | | |
| | | 43.2 | 17.6 | 30.7 | | | | |
| | | 41.4 | 15.6 | 32.5 | | | | |
| | | 19.1 | 9.8 | 29.9 | | | | |
| | | 32.4 | 10.9 | 26.8 | | | | |
| | | 31.7 | 15.6 | 26.1 | | | | |
| | | 22.0 | 6.2 | 14.4 | 1 | | 3 | mur |
| | | 40.9 | 16.3 | 27.9 | | | | |
| | | 31.3 | 10.3 | 27.5 | | | | |
| | | 22.4 | 8.4 | 17.6 | | | | |
| | | 22.5 | 5.5 | 16.5 | 1 | | 3 | nat |
| | | 33.6 | 11.8 | 26.2 | | | | |
| | | 23.7 | 9.8 | 20.5 | 1 | | 3 | mur |
| | | 17.8 | 6.4 | 14.7 | | | | |
| | | 24.6 | 6.6 | 19.5 | | | | |
| | | 35.4 | 19.1 | 30.6 | | | | |
| | | 22.7 | 6.6 | 15.8 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Rushmere Mbr. | *C. aculeata* | 15.0 | 5.6 | 12.0 | | | | |
| Lt. Run, VA | | 32.0 | 9.8 | 26.7 | | | | |
| | | 23.5 | 8.5 | 17.5 | | | | |
| | | 37.9 | 17.1 | 30.5 | | | | |
| | | 26.7 | 10.4 | 14.6 | | | | |
| | | 32.9 | 12.9 | 25.9 | | | | |
| | | 28.2 | 10.6 | 23.6 | | | | |
| | | 36.5 | 15.3 | 26.3 | | | | |
| | | 42.8 | 19.7 | 33.4 | | 1 | 1 | mur |
| | | 32.7 | 14.7 | 25.8 | | | | |
| | | 32.3 | 11.4 | 20.4 | | | | |
| | | 29.3 | 11.9 | 20.6 | | | | |
| | | 25.4 | 9.8 | 21.8 | | | | |
| | | 23.4 | 7.3 | 18.3 | | | | |
| | | 17.8 | 6.2 | 12.0 | | | | |
| | | 51.6 | 17.3 | 42.1 | | | | |
| | | 43.6 | 18.5 | 32.7 | 1 | | 3 | mur |
| | | 32.8 | 13.7 | 28.2 | | | | |
| | | 28.3 | 11.5 | 21.6 | | | | |
| | | 32.6 | 15.9 | 28.6 | | | | |
| | | 37.6 | 20.6 | 29.0 | 1 | | 1 | mur |
| | | 17.6 | 4.7 | 13.5 | | | | |
| | | 44.4 | 20.4 | 32.7 | | | | |
| | | 36.4 | 15.9 | 27.0 | | | | |
| | | 40.5 | 14.5 | 31.3 | 1 | | 3 | nat |
| | | 40.6 | 16.5 | 32.0 | | | | |
| | | 23.9 | 9.2 | 17.3 | | | | |
| | | 23.3 | 7.1 | 20.1 | | | | |
| | | 26.9 | 9.0 | 20.0 | | | | |
| | | 33.7 | 16.0 | 27.6 | | | | |
| | | 26.3 | 8.8 | 16.9 | | | | |
| | | 28.4 | 8.5 | 22.8 | | | | |
| | | 20.1 | 5.6 | 11.6 | | | | |
| | | 27.2 | 10.1 | 18.3 | | | | |
| | | 18.3 | 4.8 | 14.6 | | | | |
| | | 30.4 | 11.7 | 21.7 | | | | |
| | | 24.7 | 7.1 | 18.8 | | | | |
| | | 36.4 | 11.8 | 27.3 | | | | |
| | | 28.1 | 12.6 | 23.1 | | | | |
| | | 35.9 | 12.8 | 31.0 | | | | |
| | | 30.4 | 5.9 | 24.9 | 2 | | 3 | nat |
| | | 24.1 | 8.5 | 16.5 | | | | |
| | | 25.0 | 11.2 | 19.4 | | | | |
| | | 13.9 | 4.2 | 10.0 | 1 | | 4 | mur |
| | | **30.0** | **11.4** | **23.2** | | | | |
| | | | | | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Rushmere Mbr. | *C. plana* | 26.4 | 4.0 | 20.3 | | | | |
| Lt. Run, VA | | **26.4** | **4.0** | **20.3** | | | | |
| | | | | | | | | |
| | *C. convexa* | 42.8 | 23.3 | 28.1 | | | | |
| | | **42.8** | **23.3** | **28.1** | | | | |
| | | | | | | | | |
| | | | | | | | | |
| Moore House Mbr. | *C. fornicata* | 34.4 | 11.0 | 23.5 | 1 | | 3 | nat |
| Chuckatuck, VA | | 38.9 | 14.9 | 29.7 | | | | |
| | | 43.7 | 15.2 | 32.1 | | | | |
| | | 38.2 | 16.3 | 26.4 | 1 | | 3 | mur |
| | | 42.2 | 11.1 | 26.7 | | | | |
| | | 33.6 | 11.7 | 24.6 | | | | |
| | | 30.8 | 11.5 | 20.1 | | | | |
| | | 31.7 | 8.0 | 21.9 | | 3 | 1,3(2) | all mur |
| | | 29.1 | 13.0 | 20.7 | | | | |
| | | 37.2 | 15.3 | 25.7 | | | | |
| | | 41.5 | 14.8 | 29.3 | | | | |
| | | 37.3 | 15.5 | 26.3 | | | | |
| | | 33.7 | 10.3 | 23.0 | | | | |
| | | 44.5 | 15.9 | 30.3 | | | | |
| | | 27.0 | 9.9 | 21.0 | | | | |
| | | 26.9 | 7.8 | 21.4 | | | | |
| | | 32.6 | 12.3 | 25.2 | | | | |
| | | 48.1 | 16.2 | 36.6 | | | | |
| | | 39.3 | 11.7 | 29.8 | | | | |
| | | 33.1 | 10.2 | 20.2 | | | | |
| | | 27.7 | 11.5 | 21.0 | | | | |
| | | 18.9 | 5.3 | 12.3 | 1 | | 3 | mur |
| | | 17.9 | 7.6 | 11.6 | 1 | | 4 | mur |
| | | 20.2 | 7.0 | 14.4 | | | | |
| | | 19.6 | 6.6 | 15.6 | | | | |
| | | 16.6 | 5.2 | 11.0 | 2 | | 1,3 | 1-mur, 3-nat |
| | | 16.8 | 5.3 | 11.4 | 1 | | 3 | mur |
| | | 18.6 | 6.4 | 13.9 | | | | |
| | | 17.4 | 4.5 | 13.6 | | | | |
| | | 29.2 | 10.0 | 19.1 | | | | |
| | | 18.3 | 6.3 | 10.4 | | | | |
| | | 19.3 | 6.7 | 11.5 | | | | |
| | | 32.4 | 9.4 | 22.6 | | 1 | 3 | mur |
| | | 43.9 | 19.4 | 27.8 | | | | |
| | | 19.7 | 4.6 | 15.4 | | | | |
| | | 14.8 | 4.9 | 8.8 | | | | |
| | | 16.7 | 6.8 | 12.3 | | | | |
| | | 10.8 | 3.7 | 7.8 | | | | |
| | | 24.3 | 7.3 | 19.2 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Moore House Mbr. | *C. fornicata* | 20.2 | 5.0 | 15.1 | | | | |
| Chuckatuck, VA | | 23.8 | 9.5 | 15.5 | | | | |
| | | 20.3 | 6.7 | 12.3 | | | | |
| | | 28.2 | 10.1 | 18.8 | 1 | | 2 | mur |
| | | 18.7 | 7.8 | 12.5 | | | | |
| | | 37.6 | 17.6 | 21.5 | | | | |
| | | 31.8 | 11.9 | 22.8 | | | | |
| | | 34.1 | 13.0 | 23.3 | | | | |
| | | 18.2 | 5.3 | 11.9 | | | | |
| | | 16.7 | 7.1 | 11.8 | 1 | | 1 | nat |
| | | 27.7 | 11.4 | 21.2 | | | | |
| | | 17.7 | 5.6 | 12.7 | | | | |
| | | 39.6 | 17.1 | 27.2 | | | | |
| | | 18.7 | 5.4 | 14.0 | | | | |
| | | 29.3 | 10.1 | 22.3 | 1 | | 2 | nat |
| | | 17.0 | 4.8 | 12.5 | | | | |
| | | 18.5 | 6.9 | 11.0 | | | | |
| | | 28.6 | 11.0 | 20.3 | | | | |
| | | 36.3 | 8.5 | 24.8 | | | | |
| | | 19.8 | 6.4 | 14.6 | | 1 | 1 | mur |
| | | 12.6 | 4.4 | 7.8 | | | | |
| | | 26.3 | 8.1 | 18.6 | | | | |
| | | 19.8 | 5.0 | 12.8 | | 1 | 3 | mur |
| | | 34.7 | 8.2 | 21.3 | | 1 | 1 | mur |
| | | 37.3 | 17.4 | 26.3 | | | | |
| | | 22.7 | 7.9 | 14.6 | | | | |
| | | 15.0 | 4.9 | 9.5 | | | | |
| | | 25.8 | 8.9 | 16.7 | | | | |
| | | 16.2 | 4.5 | 10.4 | | | | |
| | | 23.6 | 8.1 | 11.9 | | | | |
| | | 42.5 | 18.5 | 26.4 | 1 | | 4 | nat |
| | | 18.4 | 6.8 | 12.0 | 2 | | 3,4 | both mur |
| | | 18.3 | 6.4 | 13.4 | | | | |
| | | 19.0 | 5.8 | 12.8 | 1 | | 3 | nat |
| | | 19.3 | 5.1 | 12.7 | | | | |
| | | 12.4 | 2.7 | 8.8 | | | | |
| | | 12.4 | 4.2 | 8.6 | | | | |
| | | 28.0 | 8.4 | 21.1 | | | | |
| | | 24.0 | 7.8 | 17.2 | | | | |
| | | 21.2 | 9.5 | 15.4 | | | | |
| | | 24.9 | 7.4 | 16.7 | 2 | | 3 | mur |
| | | 16.8 | 5.7 | 12.5 | | | | |
| | | 15.0 | 4.3 | 10.7 | | | | |
| | | 18.8 | 8.1 | 14.6 | | | | |
| | | 22.8 | 9.7 | 15.1 | | | | |
| | | 17.4 | 6.8 | 13.8 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Moore House Mbr. | *C. fornicata* | 29.2 | 7.0 | 20.5 | | | | |
| Chuckatuck, VA | | 32.0 | 11.5 | 22.5 | 1 | | 2 | mur |
| | | 35.8 | 18.5 | 25.7 | | | | |
| | | 22.2 | 4.9 | 15.7 | | | | |
| | | 22.6 | 10.7 | 14.9 | | | | |
| | | 18.5 | 8.9 | 11.4 | | 1 | 1 | mur |
| | | 25.2 | 9.1 | 14.9 | | | | |
| | | 16.0 | 5.4 | 12.3 | | | | |
| | | 36.3 | 16.6 | 27.9 | | | | |
| | | 38.4 | 18.0 | 28.4 | | | | |
| | | 29.7 | 12.5 | 20.2 | | | | |
| | | 27.1 | 8.0 | 23.0 | | | | |
| | | 20.2 | 7.0 | 13.3 | | | | |
| | | 22.1 | 6.8 | 14.8 | 2 | | 3,5 | both mur |
| | | 24.5 | 9.2 | 18.0 | | | | |
| | | 18.0 | 7.4 | 12.9 | | | | |
| | | 21.4 | 7.4 | 13.6 | | | | |
| | | 13.4 | 5.5 | 9.1 | 1 | | 3 | nat |
| | | 19.4 | 5.0 | 16.5 | | | | |
| | | 14.3 | 4.3 | 8.6 | 1 | | 3 | nat |
| | | 18.3 | 5.0 | 14.8 | | | | |
| | | 20.6 | 5.5 | 17.0 | | | | |
| | | 20.6 | 6.1 | 15.1 | | | | |
| | | 14.5 | 4.0 | 10.7 | 1 | | 3 | nat |
| | | 13.8 | 4.0 | 10.7 | | | | |
| | | 12.8 | 3.6 | 9.2 | | | | |
| | | 13.7 | 3.2 | 10.6 | | | | |
| | | 11.1 | 3.0 | 8.0 | | | | |
| | | 16.2 | 5.0 | 11.3 | | | | |
| | | 21.0 | 7.5 | 14.1 | | | | |
| | | 15.5 | 4.3 | 11.7 | | | | |
| | | 16.6 | 5.3 | 12.5 | | | | |
| | | 22.9 | 7.1 | 17.4 | | | | |
| | | 17.0 | 6.1 | 12.9 | | | | |
| | | 12.8 | 3.7 | 9.5 | | | | |
| | | 16.9 | 5.1 | 11.5 | | | | |
| | | 13.2 | 3.8 | 10.3 | | | | |
| | | **24.3** | **8.5** | **17.0** | | | | |
| | | | | | | | | |
| | *C. aculeata* | 41.1 | 22.7 | 28.3 | 1 | | 3 | nat |
| | | 47.2 | 17.1 | 40.8 | | | | |
| | | 34.3 | 16.5 | 26.7 | 1 | | 3 | mur |
| | | 42.6 | 17.9 | 32.6 | | | | |
| | | 46.9 | 17.9 | 36.6 | | | | |
| | | 36.6 | 15.2 | 27.6 | | | | |
| | | 27.0 | 13.8 | 19.2 | | | | |

| **Strat. Interval** | **Species** | **L** | **H** | **W** | **CD** | **ID** | **Dr. Loc.** | **Dr. Type** |
|---|---|---|---|---|---|---|---|---|
| Moore House Mbr. | *C. aculeata* | 17.1 | 5.6 | 13.2 | | | | |
| Chuckatuck, VA | | 37.2 | 22.0 | 29.5 | | | | |
| | | 29.8 | 10.4 | 24.1 | | | | |
| | | 30.7 | 10.4 | 24.4 | | | | |
| | | 25.5 | 10.3 | 18.9 | | | | |
| | | 30.1 | 14.1 | 25.5 | | 1 | 3 | mur |
| | | 31.2 | 11.5 | 22.8 | | | | |
| | | 21.0 | 8.6 | 16.2 | | | | |
| | | 30.2 | 12.9 | 22.6 | | | | |
| | | 13.1 | 3.6 | 10.9 | | | | |
| | | 23.8 | 9.8 | 19.5 | 1 | | 1 | nat |
| | | 22.0 | 9.4 | 15.2 | | | | |
| | | 32.2 | 13.0 | 23.0 | | | | |
| | | 25.7 | 12.0 | 20.1 | | | | |
| | | 22.8 | 6.8 | 18.4 | | | | |
| | | 22.6 | 4.4 | 18.3 | | | | |
| | | 32.7 | 15.7 | 21.2 | | | | |
| | | 17.6 | 6.6 | 13.5 | | | | |
| | | 25.2 | 9.4 | 17.0 | | | | |
| | | 16.3 | 4.7 | 12.7 | | | | |
| | | 35.8 | 10.5 | 28.4 | | | | |
| | | 28.0 | 12.9 | 22.2 | | 1 | 2 | mur |
| | | 30.6 | 8.6 | 19.6 | | | | |
| | | 36.0 | 15.0 | 30.4 | | | | |
| | | 19.4 | 7.7 | 15.2 | | | | |
| | | 27.8 | 7.8 | 20.5 | | | | |
| | | 24.5 | 6.3 | 18.7 | | | | |
| | | 30.0 | 13.0 | 18.3 | | | | |
| | | 24.4 | 8.8 | 18.6 | | | | |
| | | 36.9 | 8.7 | 26.5 | | | | |
| | | 30.7 | 17.2 | 21.6 | | | | |
| | | 31.9 | 9.7 | 21.4 | | | | |
| | | 37.9 | 11.0 | 35.5 | | | | |
| | | 31.4 | 15.3 | 20.0 | | | | |
| | | 42.1 | 15.7 | 30.6 | | | | |
| | | 21.2 | 6.1 | 15.4 | | | | |
| | | 16.6 | 5.2 | 13.7 | | | | |
| | | 27.5 | 5.4 | 22.5 | | | | |
| | | 27.8 | 10.1 | 19.6 | | | | |
| | | 40.1 | 21.9 | 27.1 | 1 | | 5 | mur |
| | | 22.9 | 5.0 | 18.0 | | | | |
| | | 26.0 | 10.9 | 19.1 | | | | |
| | | 38.0 | 17.3 | 26.5 | | | | |
| | | 31.6 | 11.2 | 24.7 | | | | |
| | | 23.6 | 10.2 | 21.2 | | | | |
| | | 27.9 | 12.9 | 17.7 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Moore House Mbr. | *C. aculeata* | 28.3 | 9.0 | 22.9 | | | | |
| Chuckatuck, VA | | 31.7 | 16.4 | 23.0 | | | | |
| | | 43.6 | 18.9 | 34.1 | | | | |
| | | 15.3 | 4.4 | 11.8 | | | | |
| | | 14.1 | 4.4 | 12.4 | | | | |
| | | 24.6 | 6.8 | 17.1 | | | | |
| | | 35.4 | 15.9 | 30.7 | | | | |
| | | 38.9 | 20.6 | 27.9 | 1 | | 3 | nat |
| | | 45.8 | 20.0 | 32.6 | | | | |
| | | 23.2 | 9.0 | 17.6 | | | | |
| | | 36.2 | 15.7 | 25.3 | | | | |
| | | 32.5 | 15.0 | 24.1 | | | | |
| | | 28.0 | 10.3 | 20.6 | | | | |
| | | 15.7 | 6.2 | 13.4 | | | | |
| | | 19.2 | 5.4 | 11.0 | | | | |
| | | 19.3 | 4.9 | 14.9 | | | | |
| | | **29.1** | **11.4** | **21.9** | | | | |
| | | | | | | | | |
| | *C. convexa* | 29.6 | 11.4 | 18.4 | | | | |
| | | 31.6 | 11.8 | 19.9 | | | | |
| | | 25.2 | 11.6 | 15.1 | | | | |
| | | 25.6 | 10.4 | 17.9 | | | | |
| | | 20.1 | 7.5 | 13.3 | | | | |
| | | 15.6 | 7.5 | 10.4 | | | | |
| | | **24.6** | **10.0** | **15.8** | | | | |
| | | | | | | | | |
| Chowan River Fm. | *C. fornicata* | 46.4 | 13.6 | 31.7 | | | | |
| Gomez Pit, VA | | 37.1 | 13.7 | 26.7 | | | | |
| | | 42.6 | 10.5 | 32.2 | | | | |
| | | 21.9 | 7.3 | 17.1 | | | | |
| | | 37.3 | 9.9 | 30.7 | | | | |
| | | 15.6 | 6.3 | 11.6 | | | | |
| | | 12.6 | 4.2 | 9.5 | | | | |
| | | 13.0 | 3.2 | 9.6 | | | | |
| | | 11.4 | 2.3 | 8.4 | | | | |
| | | 39.3 | 7.1 | 27.1 | | | | |
| | | 32.3 | 6.0 | 23.4 | | | | |
| | | 22.6 | 7.8 | 18.1 | | | | |
| | | 35.3 | 13.0 | 27.5 | | | | |
| | | 36.2 | 12.2 | 31.3 | | | | |
| | | 8.8 | 2.3 | 6.6 | | 1 | 3 | mur |
| | | 26.3 | 6.6 | 21.0 | | | | |
| | | 21.2 | 4.2 | 16.4 | | | | |
| | | 15.1 | 3.7 | 10.9 | | | | |
| | | 20.9 | 5.6 | 16.7 | | | | |
| | | 18.6 | 4.7 | 14.3 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Chowan River Fm. | *C. fornicata* | 15.8 | 4.5 | 11.9 | | | | |
| Gomez Pit, VA | | 15.8 | 3.9 | 10.9 | | | | |
| | | 24.7 | 5.0 | 16.5 | | | | |
| | | 14.8 | 4.0 | 11.5 | | | | |
| | | 17.9 | 4.3 | 12.4 | | | | |
| | | 9.7 | 3.5 | 7.2 | | | | |
| | | 16.2 | 5.5 | 12.2 | 1 | | 3 | nat |
| | | 24.2 | 9.1 | 16.7 | | | | |
| | | 23.7 | 7.1 | 18.6 | | | | |
| | | 40.8 | 13.2 | 31.5 | 1 | | 3 | nat |
| | | 12.1 | 4.1 | 8.8 | | | | |
| | | 20.4 | 7.7 | 15.5 | | | | |
| | | 14.5 | 4.2 | 10.0 | | | | |
| | | 12.6 | 3.7 | 9.7 | | | | |
| | | 15.0 | 4.5 | 11.6 | | | | |
| | | 11.2 | 4.1 | 8.3 | | | | |
| | | 10.1 | 2.6 | 7.6 | 1 | | 3 | nat |
| | | 11.4 | 3.4 | 8.5 | | | | |
| | | 33.0 | 14.9 | 23.7 | | 1 | 1 | mur |
| | | 33.2 | 14.3 | 24.0 | | | | |
| | | 40.3 | 17.8 | 30.8 | | | | |
| | | 29.0 | 14.8 | 21.5 | | | | |
| | | 23.9 | 10.3 | 16.0 | | | | |
| | | 30.8 | 11.7 | 23.8 | 1 | | 1 | mur |
| | | 25.9 | 9.8 | 20.2 | | | | |
| | | 21.0 | 9.5 | 15.3 | | | | |
| | | 25.8 | 10.3 | 19.1 | 1 | | 3 | nat |
| | | 33.9 | 13.3 | 21.9 | | | | |
| | | 24.9 | 12.3 | 18.1 | | | | |
| | | 28.8 | 15.0 | 19.9 | | | | |
| | | 27.5 | 11.8 | 18.4 | | | | |
| | | 31.1 | 12.3 | 22.6 | | | | |
| | | **23.7** | **8.0** | **17.6** | | | | |
| | | | | | | | | |
| | *C. plana* | 35.3 | 4.1 | 19.3 | | | | |
| | | 41.4 | 7.5 | 29.8 | | | | |
| | | 32.8 | 4.4 | 18.6 | | | | |
| | | 44.4 | 3.7 | 28.1 | | | | |
| | | 26.7 | 6.2 | 21.8 | | | | |
| | | 24.6 | 4.3 | 16.9 | | | | |
| | | 50.6 | 8.5 | 34.9 | | | | |
| | | 37.4 | 3.5 | 20.7 | | | | |
| | | 34.9 | 5.1 | 18.3 | | | | |
| | | 30.5 | 5.5 | 20.7 | | | | |
| | | 28.2 | 5.0 | 19.2 | | | | |
| | | 35.1 | 6.4 | 25.6 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Chowan River Fm. | *C. plana* | 35.1 | 3.8 | 18.8 | | | | |
| Gomez Pit, VA | | 27.2 | 5.2 | 20.2 | | | | |
| | | 38.5 | 8.0 | 23.7 | | | | |
| | | 36.8 | 6.5 | 25.0 | | | | |
| | | 33.1 | 5.4 | 19.4 | | | | |
| | | 14.9 | 3.0 | 9.1 | | | | |
| | | 28.4 | 2.3 | 15.4 | | | | |
| | | 28.1 | 4.8 | 23.3 | | | | |
| | | 38.7 | 7.1 | 26.0 | | | | |
| | | 25.7 | 2.8 | 14.4 | | | | |
| | | 34.1 | 4.0 | 20.7 | | | | |
| | | 23.9 | 2.6 | 14.3 | | | | |
| | | 30.9 | 6.4 | 17.9 | | | | |
| | | 20.2 | 3.9 | 16.7 | | | | |
| | | 21.8 | 4.3 | 17.6 | | | | |
| | | 23.5 | 3.9 | 13.0 | | | | |
| | | 17.7 | 3.3 | 10.0 | | | | |
| | | 18.1 | 2.5 | 13.4 | | | | |
| | | 19.4 | 1.9 | 12.2 | | | | |
| | | 23.7 | 4.8 | 18.2 | | | | |
| | | 14.5 | 3.2 | 9.7 | | | | |
| | | 10.2 | 1.6 | 7.6 | | | | |
| | | 44.4 | 9.9 | 31.2 | 1 | | 5 | mur |
| | | 36.2 | 5.4 | 21.1 | | 1 | 4 | mur |
| | | 15.0 | 3.1 | 10.9 | | | | |
| | | 14.8 | 3.2 | 10.7 | | | | |
| | | 33.2 | 5.2 | 24.1 | 1 | | 3 | nat |
| | | **29.0** | **4.7** | **18.9** | | | | |
| | | | | | | | | |
| | *C. convexa* | 37.2 | 17.5 | 25.1 | | | | |
| | | 29.4 | 14.2 | 22.6 | | | | |
| | | 22.3 | 7.6 | 15.2 | | | | |
| | | 37.2 | 19.4 | 24.5 | | | | |
| | | 31.4 | 14.4 | 22.4 | | | | |
| | | 36.2 | 17.9 | 20.6 | | | | |
| | | 37.2 | 18.2 | 24.6 | | | | |
| | | 30.5 | 13.2 | 20.7 | | | | |
| | | 34.9 | 17.5 | 22.5 | | 1 | 2 | mur |
| | | 30.1 | 13.8 | 21.7 | | | | |
| | | 34.5 | 12.9 | 23.6 | | | | |
| | | 16.4 | 5.8 | 12.0 | | 1 | 3 | nat |
| | | 9.0 | 3.3 | 6.5 | 1 | | 3 | nat |
| | | 9.8 | 3.4 | 6.8 | | | | |
| | | 11.6 | 5.1 | 7.7 | | | | |
| | | 12.4 | 4.2 | 8.8 | | | | |
| | | **26.3** | **11.8** | **17.8** | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Waccamaw Fm. | *C. fornicata* | 33.4 | 17.0 | 21.5 | | | | |
| Old Dock, NC | | 27.7 | 13.6 | 13.4 | | | | |
| | | 35.1 | 15.8 | 23.1 | | | | |
| | | 35.7 | 13.8 | 22.1 | | | | |
| | | 37.3 | 13.1 | 26.1 | 1 | | 3 | nat |
| | | 34.0 | 16.4 | 17.8 | | | | |
| | | 23.6 | 7.8 | 13.9 | | | | |
| | | 37.6 | 15.7 | 17.4 | | | | |
| | | 40.5 | 18.3 | 19.0 | | | | |
| | | 38.3 | 15.3 | 23.1 | | 1 | 1 | mur |
| | | 51.7 | 21.2 | 29.4 | | | | |
| | | 39.6 | 18.4 | 27.8 | | | | |
| | | 29.0 | 10.8 | 17.1 | | 1 | 2 | mur |
| | | 25.1 | 7.3 | 17.9 | 1 | | 3 | mur |
| | | 39.7 | 16.9 | 25.1 | | | | |
| | | 38.3 | 18.6 | 26.5 | | | | |
| | | 31.1 | 14.7 | 18.8 | | | | |
| | | 46.2 | 29.3 | 25.4 | 1 | | 5 | nat |
| | | 48.3 | 20.3 | 26.7 | | | | |
| | | 32.7 | 13.3 | 19.2 | | | | |
| | | 35.7 | 15.6 | 20.8 | | | | |
| | | 32.1 | 14.0 | 17.7 | | | | |
| | | 44.3 | 20.1 | 21.7 | | | | |
| | | 30.9 | 17.8 | 21.6 | | | | |
| | | 36.1 | 14.0 | 22.9 | | | | |
| | | 60.1 | 21.4 | 34.7 | | | | |
| | | 35.8 | 15.9 | 22.8 | | 1 | 1 | mur |
| | | 34.5 | 14.0 | 21.2 | | | | |
| | | 31.3 | 12.6 | 19.5 | | | | |
| | | 34.2 | 12.5 | 19.8 | | | | |
| | | 40.2 | 16.5 | 24.9 | | | | |
| | | 52.7 | 26.2 | 29.9 | 3 | | 1,3,5 | 1,3-nat; 5-mur |
| | | 43.3 | 17.9 | 24.5 | 1 | | 5 | nat |
| | | 40.5 | 17.9 | 23.3 | 1 | | 4 | nat |
| | | 38.5 | 16.4 | 27.3 | | | | |
| | | 26.9 | 11.3 | 15.7 | | | | |
| | | 38.9 | 13.7 | 21.8 | | | | |
| | | 30.4 | 12.9 | 16.8 | | | | |
| | | 32.7 | 12.1 | 20.2 | | 1 | 4 | mur |
| | | 30.9 | 13.2 | 18.2 | | | | |
| | | 23.1 | 10.4 | 17.2 | | | | |
| | | 21.5 | 8.7 | 13.5 | | | | |
| | | 34.9 | 12.9 | 23.0 | | | | |
| | | 35.8 | 13.9 | 22.8 | | 1 | 3 | mur |
| | | 43.3 | 17.6 | 24.8 | | | | |
| | | 25.6 | 11.3 | 15.4 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Waccamaw Fm. | *C. fornicata* | 39.3 | 14.9 | 26.5 | | | | |
| Old Dock, NC | | 45.8 | 20.7 | 26.5 | | | | |
| | | 33.5 | 13.7 | 22.7 | | | | |
| | | 33.9 | 13.5 | 23.6 | | | | |
| | | 36.6 | 15.1 | 19.6 | | | | |
| | | 47.3 | 19.1 | 28.2 | | | | |
| | | 39.4 | 17.3 | 24.8 | | | | |
| | | 36.3 | 12.7 | 23.6 | | | | |
| | | 37.7 | 16.3 | 23.3 | | | | |
| | | 30.8 | 13.2 | 21.6 | | | | |
| | | 46.7 | 20.1 | 30.1 | | | | |
| | | 45.5 | 15.3 | 26.0 | | | | |
| | | 32.3 | 14.3 | 20.4 | 1 | | 3 | nat |
| | | 32.4 | 14.9 | 22.6 | | | | |
| | | 25.5 | 10.7 | 16.4 | | | | |
| | | 30.7 | 10.5 | 18.7 | | | | |
| | | 33.9 | 13.5 | 23.0 | | | | |
| | | 38.1 | 19.1 | 25.3 | | | | |
| | | 36.2 | 14.9 | 27.3 | | | | |
| | | 30.5 | 12.4 | 18.6 | 1 | | 5 | nat |
| | | 44.0 | 17.6 | 29.3 | | | | |
| | | 30.5 | 12.9 | 18.4 | | | | |
| | | 33.7 | 11.7 | 16.0 | | | | |
| | | 35.5 | 14.5 | 18.7 | | | | |
| | | 32.6 | 13.4 | 21.4 | | | | |
| | | 37.3 | 18.6 | 23.7 | 1 | | 3 | nat |
| | | 42.2 | 20.0 | 26.5 | 2 | | 3 | nat |
| | | 33.0 | 9.2 | 23.5 | | | | |
| | | 37.6 | 13.8 | 24.4 | | | | |
| | | 27.8 | 10.7 | 15.3 | | | | |
| | | 35.8 | 16.5 | 18.1 | | | | |
| | | 35.6 | 14.5 | 23.5 | | 1 | 1 | nat |
| | | 35.0 | 14.8 | 21.3 | | | | |
| | | 37.1 | 15.0 | 23.0 | | | | |
| | | 39.4 | 16.9 | 24.2 | | | | |
| | | 36.1 | 14.7 | 18.8 | | | | |
| | | 43.1 | 17.9 | 19.5 | | | | |
| | | 33.2 | 9.8 | 21.8 | | 1 | 1 | mur |
| | | 35.5 | 15.2 | 22.0 | | | | |
| | | 43.6 | 17.4 | 27.0 | 1 | | 1 | nat |
| | | 38.4 | 15.7 | 20.2 | | | | |
| | | 33.5 | 13.1 | 20.1 | | | | |
| | | 39.6 | 15.0 | 26.8 | | | | |
| | | 41.9 | 21.8 | 26.4 | | | | |
| | | 40.2 | 15.4 | 18.5 | | | | |
| | | 41.7 | 19.8 | 23.1 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Waccamaw Fm. | *C. fornicata* | 39.5 | 14.8 | 21.6 | | | | |
| Old Dock, NC | | 32.5 | 13.4 | 15.8 | | | | |
| | | 28.3 | 10.6 | 17.6 | | | | |
| | | 32.2 | 14.9 | 16.1 | | | | |
| | | 37.0 | 15.0 | 21.6 | | | | |
| | | 34.8 | 14.1 | 21.0 | 1 | | 4 | nat |
| | | 43.2 | 18.8 | 19.9 | | | | |
| | | 38.9 | 16.1 | 20.8 | | | | |
| | | 34.5 | 18.3 | 16.9 | | | | |
| | | 38.9 | 13.7 | 17.6 | | | | |
| | | 42.8 | 20.9 | 26.6 | | | | |
| | | 55.0 | 21.9 | 26.0 | | | | |
| | | 34.6 | 11.7 | 19.3 | | | | |
| | | 34.9 | 14.5 | 24.0 | 1 | | 4 | nat |
| | | 33.9 | 15.4 | 16.5 | | | | |
| | | 29.1 | 12.2 | 14.8 | | | | |
| | | 37.5 | 17.6 | 26.2 | | | | |
| | | 34.4 | 13.6 | 22.0 | | | | |
| | | 25.2 | 9.7 | 14.5 | | | | |
| | | 46.4 | 13.0 | 28.4 | | | | |
| | | 47.3 | 17.0 | 30.9 | 1 | | 4 | nat |
| | | 43.4 | 17.4 | 20.5 | | | | |
| | | 39.6 | 16.5 | 22.7 | | | | |
| | | 34.3 | 15.1 | 19.7 | | 3 | 5 | mur |
| | | 34.9 | 14.7 | 21.0 | | | | |
| | | 21.6 | 8.5 | 12.0 | | | | |
| | | 31.5 | 10.8 | 20.9 | | | | |
| | | 27.2 | 9.2 | 17.7 | 1 | | 2 | mur |
| | | 46.8 | 19.9 | 32.2 | | | | |
| | | 38.6 | 15.9 | 17.6 | | | | |
| | | 43.4 | 15.9 | 18.8 | | | | |
| | | 43.1 | 16.9 | 18.3 | 1 | | 3 | mur |
| | | 38.6 | 18.3 | 22.2 | 1 | | 3 | nat |
| | | 33.0 | 14.3 | 16.6 | 1 | | 3 | nat |
| | | 34.6 | 11.5 | 22.4 | | | | |
| | | 34.8 | 16.7 | 20.8 | | | | |
| | | 47.4 | 21.3 | 25.0 | | | | |
| | | 35.4 | 14.3 | 25.5 | | | | |
| | | 22.0 | 7.6 | 14.3 | | | | |
| | | 45.5 | 15.1 | 22.2 | | | | |
| | | 42.0 | 18.6 | 22.4 | | 1 | 1 | nat |
| | | 31.1 | 14.6 | 14.8 | | | | |
| | | 52.9 | 16.0 | 43.2 | | 1 | 3 | nat |
| | | 53.9 | 16.5 | 44.8 | | | | |
| | | 52.5 | 17.4 | 40.7 | | | | |
| | | 18.0 | 6.7 | 12.2 | 1 | | 4 | mur |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Waccamaw Fm. | *C. fornicata* | **36.8** | **15.2** | **22.0** | | | | |
| Old Dock, NC | | | | | | | | |
| | | | | | | | | |
| Waccamaw Fm. | *C. fornicata* | 46.0 | 17.9 | 27.0 | | | | |
| Shallotte, NC | | 47.4 | 21.9 | 30.7 | | | | |
| | | 24.8 | 10.1 | 13.5 | 2 | 3 | cd-1,2; id-1,2,4 | all mur |
| | | 31.1 | 11.6 | 17.3 | | | | |
| | | 15.8 | 6.7 | 11.0 | | | | |
| | | 27.2 | 11.6 | 16.6 | | | | |
| | | 26.7 | 10.7 | 15.5 | 1 | 4 | cd-2, id-1,3(2),5 | all mur |
| | | 42.8 | 18.7 | 26.7 | | | | |
| | | 29.9 | 12.3 | 21.7 | | | | |
| | | 37.8 | 15.9 | 18.6 | 1 | | 3 | nat |
| | | 36.9 | 19.8 | 19.0 | | | | |
| | | 34.5 | 13.8 | 19.1 | | | | |
| | | 33.5 | 14.3 | 15.8 | 1 | 3 | cd-4, id-5(3) | all mur |
| | | 36.0 | 18.6 | 19.2 | | | | |
| | | 46.9 | 24.1 | 29.3 | | | | |
| | | 33.5 | 15.4 | 22.4 | | | | |
| | | 34.8 | 19.4 | 19.3 | | | | |
| | | 35.3 | 15.0 | 20.3 | | | | |
| | | 34.6 | 17.9 | 18.4 | | | | |
| | | 37.0 | 15.3 | 19.5 | | | | |
| | | 31.6 | 14.0 | 16.4 | | | | |
| | | 26.4 | 9.8 | 15.3 | | | | |
| | | 32.7 | 15.0 | 20.7 | 1 | | 5 | mur |
| | | 35.2 | 13.8 | 18.5 | | | | |
| | | 32.8 | 12.6 | 21.6 | 1 | 1 | 3 | nat |
| | | 22.1 | 8.7 | 14.3 | | | | |
| | | 42.2 | 18.3 | 27.6 | | | | |
| | | 29.2 | 11.3 | 19.5 | 1 | | 3 | nat |
| | | 42.7 | 14.1 | 25.8 | | | | |
| | | 31.6 | 14.9 | 16.8 | | | | |
| | | 40.4 | 18.7 | 20.6 | | | | |
| | | 27.0 | 10.6 | 18.6 | | | | |
| | | 21.4 | 8.3 | 14.8 | | | | |
| | | 33.8 | 15.6 | 17.0 | | | | |
| | | 21.9 | 8.4 | 14.2 | | | | |
| | | 38.9 | 18.4 | 21.9 | | | | |
| | | 20.8 | 7.4 | 14.0 | | | | |
| | | 26.5 | 11.4 | 16.8 | | | | |
| | | 29.6 | 15.1 | 18.7 | | | | |
| | | 37.3 | 16.8 | 21.7 | 1 | | 3 | nat |
| | | 36.4 | 14.8 | 18.2 | | | | |
| | | 40.4 | 17.4 | 22.5 | | 1 | 3 | mur |
| | | 48.7 | 20.7 | 24.5 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Waccamaw Fm. | *C. fornicata* | 36.3 | 13.4 | 18.2 | | | | |
| Shallotte, NC | | 32.3 | 15.7 | 18.9 | | | | |
| | | 33.9 | 13.0 | 16.4 | | | | |
| | | 28.4 | 10.7 | 18.1 | 1 | | 1 | mur |
| | | 41.8 | 16.6 | 25.3 | | | | |
| | | 47.8 | 20.6 | 27.2 | | | | |
| | | 38.9 | 16.2 | 23.1 | | | | |
| | | 45.9 | 19.1 | 25.2 | | | | |
| | | 29.7 | 12.8 | 15.7 | | | | |
| | | 45.1 | 15.6 | 29.5 | | | | |
| | | 35.3 | 13.7 | 17.4 | | | | |
| | | 33.6 | 12.1 | 22.3 | 1 | | 3 | mur |
| | | 31.4 | 19.1 | 18.8 | | | | |
| | | 24.7 | 9.1 | 15.8 | | | | |
| | | 48.3 | 15.9 | 23.8 | | | | |
| | | 30.0 | 11.3 | 15.4 | | | | |
| | | 26.5 | 8.8 | 16.2 | 1 | 7 | cd-5, id-1,3(5),4 | all mur |
| | | 36.0 | 11.4 | 19.2 | | | | |
| | | 46.9 | 18.9 | 26.4 | | | | |
| | | 32.8 | 14.4 | 18.6 | | | | |
| | | 35.9 | 15.2 | 21.4 | | | | |
| | | 27.1 | 11.6 | 15.7 | | | | |
| | | 47.5 | 18.2 | 23.6 | | | | |
| | | 24.9 | 9.3 | 16.8 | | | | |
| | | 39.1 | 17.5 | 20.6 | | | | |
| | | 30.5 | 12.8 | 23.4 | | | | |
| | | 33.4 | 12.1 | 19.2 | | | | |
| | | 19.9 | 7.6 | 14.9 | | | | |
| | | 21.3 | 9.1 | 14.5 | | | | |
| | | 21.5 | 6.4 | 15.4 | | | | |
| | | 19.1 | 7.0 | 12.9 | | | | |
| | | 15.4 | 5.5 | 10.4 | | | | |
| | | 18.4 | 5.4 | 14.7 | | | | |
| | | 11.7 | 3.7 | 8.9 | | | | |
| | | **32.9** | **13.7** | **19.3** | | | | |
| | | | | | | | | |
| | *C. plana* | **29.9** | **5.3** | **21.4** | | | | |
| | | | | | | | | |
| | *C. convexa* | **12.5** | **5.5** | **8.7** | 1 | | 3 | nat |
| | | | | | | | | |
| James City Fm. | *C. aculeata* | 22.8 | 6.2 | 17.8 | | | | |
| Aurora, NC | | 23.4 | 5.8 | 18.7 | 1 | | 3 | mur |
| | | 30.4 | 14.6 | 24.4 | | | | |
| | | 23.1 | 7.3 | 18.2 | | | | |
| | | 22.6 | 5.7 | 17.2 | | | | |
| | | 21.0 | 8.3 | 17.2 | | | | |

| **Strat. Interval** | **Species** | **L** | **H** | **W** | **CD** | **ID** | **Dr. Loc.** | **Dr. Type** |
|---|---|---|---|---|---|---|---|---|
| James City Fm. | *C. aculeata* | 23.8 | 9.7 | 20.0 | | | | |
| Aurora, NC | | 18.5 | 6.3 | 13.9 | | | | |
| | | 22.6 | 6.8 | 17.4 | | | | |
| | | 23.5 | 9.5 | 19.8 | | | | |
| | | 22.2 | 7.3 | 17.2 | 1 | | 3 | mur |
| | | 27.1 | 7.7 | 22.6 | | | | |
| | | 29.0 | 9.1 | 22.0 | | | | |
| | | 23.7 | 6.2 | 19.7 | | 1 | 3 | mur |
| | | 21.5 | 6.8 | 18.1 | | | | |
| | | 24.7 | 7.9 | 20.9 | | 1 | 3 | mur |
| | | 26.9 | 8.7 | 19.7 | | | | |
| | | 26.7 | 12.5 | 20.4 | | | | |
| | | 25.1 | 7.9 | 21.6 | | | | |
| | | 18.0 | 8.3 | 12.5 | | | | |
| | | 20.8 | 6.4 | 17.1 | | | | |
| | | 19.2 | 6.9 | 16.4 | | | | |
| | | 25.5 | 8.1 | 22.3 | | 1 | 3 | mur |
| | | 26.5 | 9.1 | 20.1 | | | | |
| | | 22.7 | 8.6 | 18.1 | | | | |
| | | 19.4 | 4.9 | 15.8 | | | | |
| | | 23.4 | 8.4 | 16.6 | | | | |
| | | 25.2 | 8.9 | 19.4 | | | | |
| | | 21.6 | 8.9 | 14.8 | | | | |
| | | 22.4 | 6.3 | 18.5 | 1 | | 4 | nat |
| | | 18.2 | 5.5 | 16.2 | | | | |
| | | 24.1 | 9.1 | 17.8 | | | | |
| | | 21.3 | 7.2 | 16.7 | | | | |
| | | 19.8 | 8.5 | 15.6 | 1 | 1 | cd-4, id-2 | cd-mur, id-nat |
| | | 19.6 | 4.7 | 17.3 | | 1 | 3 | mur |
| | | 18.5 | 4.6 | 13.9 | | | | |
| | | 18.4 | 9.3 | 14.6 | | | | |
| | | 16.8 | 6.2 | 12.2 | 1 | | 3 | mur |
| | | 22.6 | 4.8 | 18.3 | | | | |
| | | 26.1 | 9.1 | 21.8 | | | | |
| | | 21.6 | 7.2 | 13.0 | | | | |
| | | 39.1 | 14.4 | 29.4 | | | | |
| | | 24.7 | 10.2 | 21.0 | | | | |
| | | 21.0 | 3.9 | 15.7 | 1 | 1 | cd-3, id-1 | both mur |
| | | 20.4 | 7.4 | 17.9 | | | | |
| | | 19.9 | 6.6 | 16.2 | 1 | | 2 | mur |
| | | 18.1 | 8.8 | 14.4 | | | | |
| | | 24.6 | 8.2 | 19.2 | | | | |
| | | 22.8 | 8.5 | 17.2 | | | | |
| | | 24.3 | 9.4 | 18.7 | 1 | | 3 | mur |
| | | 19.4 | 5.8 | 15.6 | | | | |
| | | 21.4 | 7.6 | 16.8 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| James City Fm. | *C. aculeata* | 20.3 | 5.7 | 16.5 | | | | |
| Aurora, NC | | 27.2 | 7.0 | 21.3 | | | | |
| | | 21.6 | 7.0 | 16.8 | | | | |
| | | 19.8 | 5.9 | 15.4 | 1 | | 3 | mur |
| | | 20.8 | 4.8 | 16.9 | | | | |
| | | 21.2 | 6.7 | 16.1 | | | | |
| | | 22.5 | 6.5 | 17.0 | | | | |
| | | 23.4 | 7.8 | 17.8 | | | | |
| | | 20.9 | 6.9 | 17.0 | | | | |
| | | 20.2 | 8.1 | 14.9 | | | | |
| | | 27.2 | 8.2 | 19.0 | | | | |
| | | 15.9 | 6.0 | 12.3 | | | | |
| | | 23.7 | 8.0 | 20.4 | | | | |
| | | 24.3 | 6.8 | 20.4 | | | | |
| | | 22.7 | 6.4 | 19.1 | | | | |
| | | 22.4 | 7.9 | 18.9 | | | | |
| | | 21.7 | 7.3 | 18.8 | 2 | | 1,3 | both mur |
| | | 17.3 | 6.0 | 14.1 | | | | |
| | | 26.6 | 8.1 | 22.5 | | | | |
| | | 20.2 | 8.1 | 17.4 | 1 | | 5 | nat |
| | | 19.6 | 8.7 | 15.9 | | | | |
| | | 20.0 | 6.3 | 16.0 | | | | |
| | | 20.1 | 6.9 | 14.5 | | | | |
| | | 22.8 | 6.8 | 17.8 | | | | |
| | | 23.6 | 7.4 | 16.5 | | | | |
| | | 16.6 | 5.0 | 14.7 | 1 | | 1 | nat |
| | | 19.5 | 6.2 | 15.5 | | | | |
| | | 18.8 | 8.3 | 15.7 | | | | |
| | | 26.1 | 7.6 | 20.6 | | | | |
| | | 22.5 | 5.4 | 14.1 | | | | |
| | | 21.0 | 5.8 | 15.6 | 1 | | 5 | nat |
| | | 24.4 | 7.3 | 18.8 | | | | |
| | | 19.8 | 5.9 | 15.9 | | | | |
| | | 20.3 | 6.0 | 15.6 | | | | |
| | | 14.9 | 4.2 | 11.9 | | | | |
| | | 16.7 | 4.7 | 13.9 | | | | |
| | | 16.6 | 6.8 | 14.0 | | 1 | 1 | mur |
| | | 27.9 | 9.4 | 20.2 | | | | |
| | | 22.7 | 7.5 | 20.4 | | | | |
| | | 18.8 | 5.0 | 13.6 | 1 | 1 | cd-3, id-3 | both mur |
| | | 26.5 | 8.3 | 20.3 | | | | |
| | | 25.0 | 8.3 | 20.8 | | | | |
| | | 14.7 | 5.3 | 11.9 | | | | |
| | | 23.8 | 7.2 | 21.9 | | | | |
| | | 21.4 | 5.2 | 17.6 | | | | |
| | | 20.4 | 6.9 | 15.3 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| James City Fm. | *C. aculeata* | 21.8 | 6.7 | 20.3 | | | | |
| Aurora, NC | | 24.2 | 10.4 | 18.2 | | | | |
| | | 21.5 | 6.1 | 17.4 | 2 | | 3,5 | both mur |
| | | 24.4 | 7.5 | 19.5 | | | | |
| | | 18.8 | 8.1 | 13.7 | | | | |
| | | 14.0 | 5.6 | 10.6 | | | | |
| | | 28.0 | 7.7 | 22.0 | | | | |
| | | 21.5 | 7.3 | 18.6 | | | | |
| | | 15.6 | 5.4 | 13.2 | | | | |
| | | 23.0 | 6.0 | 18.4 | 2 | | 3 | mur |
| | | 20.3 | 9.5 | 14.4 | | | | |
| | | 20.5 | 7.4 | 15.3 | | | | |
| | | 27.4 | 8.2 | 22.7 | | | | |
| | | 19.6 | 6.0 | 16.2 | | 2 | 4 | mur |
| | | 18.7 | 7.7 | 16.1 | | | | |
| | | 26.0 | 6.6 | 20.0 | | | | |
| | | 24.3 | 8.6 | 20.9 | | | | |
| | | 19.6 | 7.4 | 16.5 | 1 | | 3 | nat |
| | | 25.7 | 7.6 | 17.7 | | | | |
| | | 26.0 | 8.3 | 19.7 | | | | |
| | | 21.6 | 8.3 | 15.6 | 1 | | 3 | mur |
| | | 23.1 | 6.8 | 18.3 | | | | |
| | | **22.1** | **7.3** | **17.5** | | | | |
| | | | | | | | | |
| | *C. fornicata* | 24.8 | 9.2 | 20.1 | | 2 | 1 | mur |
| | | 37.8 | 12.7 | 30.0 | | | | |
| | | 38.5 | 12.9 | 28.0 | 1 | | 3 | mur |
| | | 41.9 | 14.9 | 31.3 | 2 | | 3,5 | both mur |
| | | 36.2 | 12.5 | 27.2 | 1 | | 3 | nat |
| | | 39.8 | 11.7 | 27.2 | | | | |
| | | 38.5 | 13.5 | 29.6 | | | | |
| | | 33.6 | 10.9 | 25.9 | 1 | | 4 | mur |
| | | 47.3 | 13.4 | 32.3 | 4 | | 3(3),5 | all mur |
| | | 39.1 | 11.8 | 27.1 | 1 | 2 | cd-2, id-3,4 | all mur |
| | | 27.4 | 9.4 | 21.9 | | | | |
| | | 32.2 | 12.6 | 24.6 | | | | |
| | | 39.1 | 14.3 | 29.7 | | | | |
| | | 41.2 | 16.8 | 33.3 | | | | |
| | | 34.0 | 11.4 | 24.7 | 1 | | 3 | nat |
| | | 35.4 | 12.2 | 27.2 | | | | |
| | | 35.1 | 10.6 | 27.6 | 1 | | 3 | mur |
| | | 27.3 | 7.0 | 21.8 | | | | |
| | | 26.3 | 6.1 | 19.3 | | | | |
| | | 26.9 | 10.4 | 18.6 | | | | |
| | | 33.7 | 13.0 | 24.6 | | | | |
| | | 34.0 | 10.8 | 25.3 | 2 | 2 | cd-3(2); id-2,5 | all mur |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| James City Fm. | *C. fornicata* | 32.5 | 11.3 | 25.1 | 1 | | 3 | nat |
| Aurora, NC | | 14.2 | 5.5 | 11.6 | | | | |
| | | 22.7 | 5.4 | 17.6 | 1 | | 3 | nat |
| | | 22.3 | 7.8 | 16.4 | | | | |
| | | 33.3 | 9.6 | 22.6 | | | | |
| | | 58.7 | 20.0 | 37.7 | | | | |
| | | 38.0 | 9.7 | 30.4 | 2 | | 3,5 | 3-mur, 5-nat |
| | | 28.5 | 8.2 | 21.6 | | | | |
| | | 32.8 | 7.8 | 25.7 | | | | |
| | | 26.8 | 6.0 | 18.2 | 1 | | 3 | mur |
| | | 25.1 | 7.2 | 19.4 | 1 | | 3 | mur |
| | | 27.0 | 9.9 | 21.9 | 1 | | 3 | nat |
| | | 45.4 | 8.4 | 33.2 | | | | |
| | | 30.8 | 7.6 | 23.8 | | | | |
| | | 35.1 | 9.8 | 29.9 | 3 | | 1(2),3 | all mur |
| | | 31.5 | 8.2 | 21.5 | | | | |
| | | 34.2 | 9.7 | 25.4 | | | | |
| | | 30.2 | 9.2 | 23.1 | 1 | | 3 | nat |
| | | 38.1 | 12.7 | 28.4 | 2 | | 3 | mur |
| | | 35.0 | 7.2 | 27.5 | | | | |
| | | 33.6 | 10.1 | 24.5 | | 2 | 3,5 | both mur |
| | | 30.2 | 8.0 | 24.1 | | | | |
| | | 25.8 | 7.9 | 19.5 | | | | |
| | | 20.9 | 4.3 | 16.9 | | | | |
| | | 23.1 | 7.0 | 17.6 | | | | |
| | | 37.6 | 10.7 | 30.5 | | | | |
| | | 33.1 | 12.0 | 24.4 | | | | |
| | | 25.1 | 6.0 | 19.2 | | | | |
| | | 30.2 | 8.6 | 22.1 | | | | |
| | | 23.3 | 7.2 | 17.7 | 1 | | 3 | mur |
| | | 27.5 | 5.0 | 21.9 | 1 | | 3 | nat |
| | | **32.5** | **9.9** | **24.5** | | | | |
| | | | | | | | | |
| | *C. plana* | 42.6 | 8.2 | 32.4 | 3 | | 2,3(2) | all mur |
| | | 40.4 | 9.1 | 32.7 | | | | |
| | | 31.6 | 5.8 | 25.5 | | | | |
| | | 22.8 | 4.4 | 15.8 | | | | |
| | | 30.6 | 5.8 | 22.5 | | | | |
| | | 36.2 | 4.8 | 28.2 | | | | |
| | | 35.6 | 7.3 | 26.0 | | 1 | 3 | mur |
| | | **34.3** | **6.5** | **26.2** | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Pinecrest Bed (#3) | *C. fornicata* | 20.5 | 5.1 | 14.2 | | | | |
| Quality Aggregates, FL | | 30.6 | 7.7 | 19.2 | | | | |
| | | 28.6 | 8.4 | 19.7 | | | | |
| | | 33.9 | 7.2 | 24.8 | | | | |
| | | 37.4 | 9.4 | 26.5 | | | | |
| | | 26.5 | 5.5 | 21.3 | | | | |
| | | 38.3 | 10.6 | 24.9 | | | | |
| | | 25.1 | 6.5 | 14.3 | | | | |
| | | 16.0 | 3.8 | 13.4 | | | | |
| | | 25.1 | 6.8 | 19.2 | | | | |
| | | 25.0 | 5.2 | 18.6 | | | | |
| | | 33.6 | 6.5 | 25.5 | 1 | | 1 | muricid |
| | | 34.1 | 10.0 | 22.4 | | | | |
| | | 37.6 | 11.2 | 23.8 | | | | |
| | | 32.0 | 7.7 | 23.9 | | | | |
| | | 16.3 | 3.2 | 10.7 | | | | |
| | | 18.3 | 5.2 | 12.6 | | | | |
| | | 21.8 | 3.1 | 17.2 | | | | |
| | | 20.8 | 3.4 | 15.9 | | | | |
| | | 29.7 | 7.6 | 18.7 | | | | |
| | | 28.4 | 5.2 | 25.1 | | | | |
| | | 14.3 | 4.9 | 10.5 | | | | |
| | | 19.3 | 5.5 | 13.1 | | | | |
| | | 19.0 | 3.7 | 14.3 | | | | |
| | | 28.8 | 7.4 | 24.7 | | | | |
| | | 23.3 | 4.7 | 15.6 | | | | |
| | | 26.5 | 6.6 | 19.2 | | | | |
| | | 41.8 | 11.9 | 22.1 | | | | |
| | | 24.5 | 6.4 | 17.7 | | | | |
| | | 25.0 | 6.4 | 18.7 | | | | |
| | | 30.7 | 8.4 | 20.3 | | | | |
| | | 26.3 | 4.5 | 20.2 | | | | |
| | | 22.6 | 6.6 | 16.9 | | | | |
| | | 20.7 | 5.6 | 14.4 | | | | |
| | | 17.8 | 3.9 | 13.3 | | | | |
| | | 17.8 | 4.1 | 14.7 | | | | |
| | | 37.9 | 7.3 | 21.0 | | | | |
| | | 31.0 | 7.9 | 20.0 | | | | |
| | | 32.5 | 8.1 | 25.4 | | 1 | 1 | mur |
| | | 31.8 | 10.9 | 19.8 | | | | |
| | | 27.7 | 7.2 | 18.9 | | 1 | 1 | mur |
| | | 20.9 | 4.9 | 16.8 | | | | |
| | | 19.9 | 5.8 | 13.6 | | | | |
| | | 30.6 | 7.3 | 17.7 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Pinecrest Bed (#3) | *C. fornicata* | 19.6 | 4.6 | 16.0 | | | | |
| Quality Aggregates, FL | | 21.7 | 4.4 | 15.7 | | | | |
| | | 12.6 | 3.1 | 8.8 | | | | |
| | | 22.4 | 3.9 | 16.7 | | | | |
| | | 16.5 | 5.2 | 12.4 | | | | |
| | | 14.6 | 3.3 | 12.9 | | | | |
| | | 27.3 | 7.8 | 22.4 | | | | |
| | | 17.4 | 4.5 | 11.4 | | | | |
| | | 35.3 | 9.0 | 23.0 | | 1 | 3 | muricid |
| | | **25.6** | **6.3** | **18.1** | | | | |
| | | | | | | | | |
| | *C. maculosa* | 11.0 | 2.9 | 8.1 | | | | |
| | | 12.0 | 4.4 | 8.1 | | | | |
| | | 20.8 | 6.9 | 16.7 | | | | |
| | | 21.0 | 6.3 | 14.6 | | | | |
| | | 19.0 | 5.1 | 12.8 | | | | |
| | | **16.8** | **5.1** | **12.1** | | | | |
| | | | | | | | | |
| Nashua Fm. | *C. plana* | 31.7 | 4.2 | 17.5 | | | | |
| Cracker Swamp, FL | | 27.4 | 5.1 | 22.5 | 1 | | 3 | mur |
| | | 25.2 | 3.5 | 22.1 | | | | |
| | | 22.1 | 4.0 | 16.4 | | | | |
| | | 29.9 | 3.1 | 17.1 | | | | |
| | | 25.1 | 4.0 | 16.8 | | | | |
| | | 32.4 | 4.8 | 16.4 | | | | |
| | | 17.5 | 1.6 | 10.5 | | | | |
| | | 27.5 | 4.8 | 19.1 | | | | |
| | | 18.0 | 1.6 | 18.5 | | | | |
| | | 25.6 | 4.1 | 12.8 | | | | |
| | | 25.1 | 2.7 | 15.5 | | | | |
| | | 13.9 | 1.0 | 12.5 | | | | |
| | | 15.7 | 1.5 | 9.4 | | | | |
| | | 13.7 | 1.2 | 8.9 | | | | |
| | | 21.1 | 2.6 | 12.6 | | | | |
| | | 14.3 | 1.6 | 8.2 | | | | |
| | | 23.6 | 3.7 | 14.5 | | | | |
| | | 18.0 | 2.1 | 9.6 | | | | |
| | | 9.0 | 1.0 | 6.3 | | | | |
| | | 9.2 | 1.0 | 7.0 | | | | |
| | | 4.7 | 0.9 | 4.8 | | | | |
| | | **20.5** | **2.7** | **13.6** | | | | |
| | | | | | | | | |
| | *C. convexa* | 33.2 | 12.8 | 24.0 | | | | |
| | | 22.0 | 9.3 | 15.1 | | | | |
| | | 23.0 | 9.6 | 17.8 | | | | |
| | | 39.9 | 18.9 | 27.7 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Nashua Fm. | *C. convexa* | 24.0 | 7.9 | 15.5 | 1 | | 3 | mur |
| Cracker Swamp, FL | | 24.3 | 10.9 | 17.0 | | | | |
| | | 25.4 | 12.2 | 14.4 | | | | |
| | | 26.4 | 11.7 | 20.0 | | | | |
| | | 23.5 | 5.0 | 15.9 | | | | |
| | | 29.0 | 13.0 | 16.5 | | | | |
| | | 26.3 | 8.3 | 19.2 | | | | |
| | | 25.8 | 8.3 | 17.9 | | | | |
| | | 29.5 | 9.8 | 19.0 | | | | |
| | | 25.8 | 9.4 | 18.3 | 1 | | 1 | nat |
| | | 20.6 | 10.8 | 14.8 | | | | |
| | | 36.2 | 11.7 | 22.6 | | | | |
| | | 13.3 | 4.8 | 9.1 | | | | |
| | | 11.4 | 5.2 | 8.6 | | | | |
| | | 21.1 | 9.0 | 13.8 | | | | |
| | | 15.7 | 5.7 | 10.4 | | | | |
| | | 17.0 | 7.7 | 11.6 | | | | |
| | | 18.5 | 6.8 | 13.3 | | | | |
| | | 17.6 | 5.8 | 9.9 | | | | |
| | | 12.5 | 4.1 | 9.0 | | | | |
| | | 11.3 | 4.6 | 6.7 | | | | |
| | | 8.6 | 3.2 | 6.0 | | | | |
| | | 7.7 | 3.8 | 4.9 | | | | |
| | | 9.0 | 2.0 | 6.3 | | | | |
| | | 10.0 | 3.0 | 7.5 | | | | |
| | | 9.4 | 3.0 | 6.1 | | | | |
| | | 4.7 | 1.5 | 3.4 | | | | |
| | | 9.9 | 2.2 | 6.7 | | | | |
| | | 7.6 | 2.5 | 5.7 | | | | |
| | | 9.1 | 3.6 | 6.3 | | | | |
| | | 10.1 | 4.0 | 7.0 | | | | |
| | | 7.8 | 2.6 | 4.5 | | | | |
| | | 6.1 | 2.6 | 4.0 | | | | |
| | | 5.8 | 2.5 | 3.3 | | | | |
| | | 4.7 | 1.9 | 3.0 | | | | |
| | | 3.8 | 1.6 | 2.2 | | | | |
| | | 4.1 | 1.4 | 2.6 | | | | |
| | | 3.5 | 1.4 | 2.8 | 1 | | 1 | mur |
| | | 19.0 | 5.4 | 11.5 | | | | |
| | | 20.9 | 7.3 | 11.9 | | | | |
| | | 14.1 | 4.6 | 9.9 | | | | |
| | | 15.8 | 5.5 | 9.8 | | | | |
| | | 10.4 | 3.3 | 7.3 | | | | |
| | | 11.5 | 3.2 | 7.7 | | | | |
| | | 12.5 | 5.0 | 8.4 | 1 | | 3 | mur |
| | | **16.7** | **6.3** | **11.2** | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Nashua Fm. | *C. fornicata* | 26.0 | 8.5 | 18.4 | | | | |
| Cracker Swamp, FL | | 16.6 | 6.6 | 10.5 | | | | |
| | | 15.8 | 3.7 | 10.9 | 2 | | 1,1 | mur |
| | | 19.3 | 5.4 | 13.7 | | | | |
| | | 14.6 | 6.0 | 10.2 | | | | |
| | | 15.1 | 3.6 | 10.9 | | | | |
| | | 6.1 | 2.3 | 4.2 | | | | |
| | | 5.9 | 2.1 | 3.9 | | | | |
| | | 13.6 | 4.8 | 8.2 | 1 | | 3 | mur |
| | | 13.1 | 4.3 | 8.4 | | | | |
| | | 11.4 | 4.4 | 7.7 | | | | |
| | | 9.4 | 3.0 | 6.4 | | | | |
| | | 13.2 | 3.8 | 7.3 | | | | |
| | | 5.2 | 1.9 | 3.4 | | | | |
| | | 6.4 | 2.1 | 3.9 | | | | |
| | | 3.5 | 1.1 | 2.5 | | | | |
| | | 3.3 | 1.2 | 2.4 | | | | |
| | | 14.1 | 4.8 | 9.0 | | | | |
| | | 8.8 | 2.8 | 5.8 | | | | |
| | | 8.1 | 3.0 | 5.4 | | | | |
| | | 9.6 | 3.1 | 6.7 | | | | |
| | | 9.8 | 3.1 | 6.3 | 1 | | 1 | mur |
| | | 10.5 | 3.2 | 6.7 | | 1 | 3 | mur |
| | | 8.1 | 2.8 | 5.2 | 1 | | 1 | mur |
| | | 7.7 | 2.2 | 5.1 | | | | |
| | | 6.3 | 2.2 | 4.3 | | | | |
| | | 5.2 | 1.4 | 4.0 | | | | |
| | | 5.8 | 1.6 | 3.9 | | | | |
| | | 5.4 | 1.9 | 4.0 | | 1 | 1 | mur |
| | | 4.3 | 1.4 | 3.3 | | | | |
| | | 5.6 | 1.9 | 4.1 | 1 | | 5 | mur |
| | | 13.8 | 4.3 | 8.9 | | | | |
| | | 12.8 | 4.9 | 8.1 | | | | |
| | | 10.8 | 3.0 | 7.3 | 1 | | 1 | mur |
| | | 10.5 | 3.0 | 7.1 | | | | |
| | | 11.9 | 3.5 | 7.7 | | | | |
| | | 12.0 | 3.8 | 7.9 | | 1 | 1 | mur |
| | | 9.2 | 3.0 | 6.8 | 1 | | 1 | mur |
| | | 10.6 | 3.5 | 6.9 | | | | |
| | | 8.5 | 2.7 | 5.8 | | | | |
| | | 10.6 | 3.1 | 6.6 | | | | |
| | | 9.7 | 2.5 | 6.5 | | | | |
| | | 11.5 | 4.3 | 8.2 | | | | |
| | | 12.9 | 4.0 | 7.5 | | | | |
| | | 8.7 | 3.4 | 5.3 | | 2 | 1,1 | mur |
| | | 10.6 | 3.6 | 7.2 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Nashua Fm. | *C. fornicata* | 12.3 | 3.4 | 8.3 | | | | |
| Cracker Swamp, FL | | 10.4 | 3.2 | 6.7 | | | | |
| | | 10.4 | 3.3 | 6.9 | | | | |
| | | 8.3 | 3.0 | 5.6 | | | | |
| | | 12.3 | 3.1 | 8.7 | | | | |
| | | 12.5 | 4.6 | 7.5 | | | | |
| | | 11.7 | 4.1 | 8.3 | | | | |
| | | 5.2 | 1.6 | 3.9 | | | | |
| | | 9.3 | 2.5 | 6.4 | | | | |
| | | 9.6 | 2.7 | 6.1 | | 1 | 1 | mur |
| | | 10.0 | 3.3 | 6.9 | | | | |
| | | 11.1 | 4.7 | 6.7 | | | | |
| | | 12.4 | 4.8 | 8.9 | | | | |
| | | 9.5 | 3.0 | 6.0 | 1 | 1 | 1,1 | mur |
| | | 11.1 | 3.8 | 6.8 | | | | |
| | | 10.1 | 3.2 | 6.6 | | | | |
| | | 10.2 | 2.9 | 7.9 | | | | |
| | | 7.2 | 2.3 | 4.0 | | | | |
| | | 4.9 | 2.7 | 3.4 | | | | |
| | | 4.4 | 1.5 | 3.0 | | | | |
| | | 6.1 | 2.1 | 4.1 | | | | |
| | | 5.0 | 1.7 | 3.1 | 1 | | 3 | mur |
| | | 14.6 | 4.7 | 9.6 | | | | |
| | | 14.4 | 4.9 | 9.5 | | | | |
| | | 8.8 | 3.1 | 6.0 | | | | |
| | | 12.4 | 5.0 | 8.0 | | | | |
| | | 12.2 | 5.2 | 7.5 | | 1 | 1 | mur |
| | | 12.7 | 4.5 | 6.4 | | | | |
| | | 7.0 | 2.2 | 4.5 | | | | |
| | | 9.6 | 3.6 | 6.7 | | 1 | 1 | mur |
| | | 10.7 | 3.1 | 7.8 | | | | |
| | | 5.6 | 1.7 | 3.9 | 1 | | 3 | mur |
| | | 10.5 | 2.9 | 7.2 | | | | |
| | | 11.4 | 3.1 | 6.9 | | | | |
| | | 11.8 | 3.8 | 8.3 | | | | |
| | | 11.0 | 2.6 | 7.4 | | | | |
| | | 12.1 | 5.2 | 6.8 | | | | |
| | | 7.5 | 2.6 | 5.2 | | | | |
| | | 7.6 | 2.8 | 5.4 | | | | |
| | | 9.4 | 2.9 | 6.9 | | | | |
| | | 11.6 | 4.5 | 7.0 | | | | |
| | | 11.1 | 3.7 | 7.1 | 1 | | 1 | mur |
| | | 9.8 | 3.4 | 6.0 | | | | |
| | | 6.5 | 2.3 | 4.8 | | | | |
| | | 7.4 | 2.2 | 4.6 | | 1 | 5 | mur |
| | | 10.7 | 3.1 | 7.6 | | 1 | 1 | mur |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Nashua Fm. | *C. fornicata* | 12.4 | 3.0 | 7.9 | | 2 | 1,1 | mur |
| Cracker Swamp, FL | | 9.6 | 3.2 | 6.3 | | | | |
| | | 9.1 | 3.5 | 5.7 | | | | |
| | | 9.8 | 3.4 | 6.2 | | | | |
| | | 11.7 | 3.7 | 8.1 | | | | |
| | | 12.6 | 3.5 | 8.4 | | | | |
| | | 11.1 | 4.1 | 7.6 | | | | |
| | | 7.8 | 2.2 | 5.0 | | | | |
| | | 5.9 | 2.3 | 3.5 | | | | |
| | | 11.3 | 3.7 | 7.3 | | | | |
| | | 11.4 | 3.2 | 7.6 | 1 | | 1 | mur |
| | | 9.6 | 2.8 | 6.5 | | 1 | 1 | mur |
| | | 11.4 | 3.7 | 7.4 | | | | |
| | | 11.8 | 3.7 | 7.5 | | | | |
| | | 11.4 | 3.7 | 7.6 | | | | |
| | | 12.1 | 3.9 | 7.9 | | | | |
| | | 13.5 | 3.9 | 8.0 | | | | |
| | | 10.0 | 2.8 | 7.0 | | | | |
| | | 10.1 | 2.5 | 6.3 | | | | |
| | | 10.7 | 3.6 | 6.6 | | | | |
| | | 7.4 | 2.4 | 5.0 | | | | |
| | | 7.7 | 2.3 | 5.0 | | | | |
| | | 9.2 | 3.1 | 6.5 | | | | |
| | | 10.1 | 3.1 | 6.8 | | | | |
| | | 10.8 | 4.0 | 6.8 | | | | |
| | | 8.8 | 2.7 | 6.3 | | | | |
| | | 10.7 | 3.1 | 7.3 | | | | |
| | | 9.0 | 3.1 | 6.3 | | | | |
| | | 10.5 | 2.4 | 8.0 | | | | |
| | | 9.6 | 3.1 | 6.7 | | | | |
| | | 10.3 | 3.8 | 6.2 | | | | |
| | | 9.9 | 2.2 | 6.8 | | | | |
| | | 14.3 | 4.0 | 9.2 | | | | |
| | | 10.7 | 3.0 | 6.5 | | | | |
| | | 11.9 | 3.1 | 7.1 | | | | |
| | | 11.0 | 3.8 | 8.0 | | | | |
| | | 10.3 | 2.9 | 7.0 | | | | |
| | | 11.9 | 3.8 | 7.7 | 1 | | 1 | nat |
| | | 7.7 | 2.4 | 5.3 | | | | |
| | | 10.8 | 4.0 | 7.8 | | | | |
| | | 4.0 | 1.1 | 3.4 | | 1 | 3 | mur |
| | | 8.3 | 2.8 | 5.3 | | | | |
| | | 9.1 | 2.8 | 6.3 | | | | |
| | | 6.9 | 2.8 | 4.9 | | | | |
| | | 7.6 | 1.9 | 5.1 | | | | |
| | | 8.9 | 2.7 | 6.6 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Nashua Fm. | *C. fornicata* | **10.0** | **3.2** | **6.7** | | | | |
| Cracker Swamp, FL | | | | | | | | |
| | | | | | | | | |
| Bermont Fm. | *C. fornicata* | 41.5 | 19.0 | 26.1 | | | | |
| Loxahatchee, FL | | 35.5 | 17.9 | 20.2 | 1 | | 5 | mur |
| | | 19.1 | 6.8 | 11.2 | | | | |
| | | 26.8 | 13.1 | 18.1 | | | | |
| | | 30.3 | 14.5 | 18.2 | | | | |
| | | 28.3 | 14.7 | 21.0 | | | | |
| | | 29.5 | 14.1 | 19.4 | | | | |
| | | 25.7 | 12.4 | 18.9 | | | | |
| | | 27.3 | 8.1 | 17.9 | | | | |
| | | 21.7 | 10.0 | 13.7 | | | | |
| | | 26.0 | 7.6 | 16.4 | | | | |
| | | 27.2 | 7.2 | 19.8 | 1 | | 5 | mur |
| | | **28.2** | **12.1** | **18.4** | | | | |
| | | | | | | | | |
| | *C. convexa* | 26.8 | 13.6 | 17.2 | | | | |
| | | 22.5 | 12.2 | 15.2 | | 1 | 5 | mur |
| | | 33.5 | 14.7 | 17.2 | | | | |
| | | 22.0 | 8.3 | 14.1 | | | | |
| | | 25.3 | 12.7 | 13.0 | | | | |
| | | 23.5 | 15.1 | 18.2 | | | | |
| | | 21.2 | 9.6 | 14.5 | | | | |
| | | 25.4 | 14.3 | 12.8 | | | | |
| | | 25.8 | 10.5 | 17.2 | | | | |
| | | 24.9 | 12.7 | 14.6 | | | | |
| | | 25.6 | 11.3 | 17.1 | | | | |
| | | 30.7 | 13.6 | 18.5 | | | | |
| | | 29.5 | 12.2 | 16.7 | | | | |
| | | 29.2 | 11.2 | 19.3 | | | | |
| | | 25.3 | 9.7 | 16.5 | | | | |
| | | 28.1 | 11.0 | 18.3 | | | | |
| | | 25.6 | 13.2 | 17.1 | | | | |
| | | 28.4 | 13.8 | 18.4 | | | | |
| | | 11.6 | 4.2 | 7.7 | | | | |
| | | 22.0 | 8.7 | 12.9 | | | | |
| | | 25.4 | 10.9 | 14.3 | | | | |
| | | 21.3 | 12.3 | 13.2 | | | | |
| | | 30.4 | 11.2 | 18.3 | | | | |
| | | 23.2 | 9.5 | 13.9 | | | | |
| | | 26.3 | 11.2 | 16.5 | | | | |
| | | 27.8 | 12.8 | 17.8 | | | | |
| | | 24.2 | 10.5 | 16.7 | | | | |
| | | 23.8 | 11.6 | 17.7 | | | | |
| | | 28.2 | 12.5 | 18.9 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Bermont Fm. | *C. convexa* | 27.0 | 11.0 | 18.4 | | | | |
| Loxahatchee, FL | | 25.3 | 11.2 | 16.0 | | | | |
| | | 20.2 | 8.2 | 12.3 | | | | |
| | | 29.3 | 10.6 | 21.0 | | | | |
| | | 27.1 | 12.4 | 15.2 | | | | |
| | | 26.7 | 13.1 | 15.6 | | | | |
| | | 26.3 | 16.0 | 14.5 | | | | |
| | | 20.1 | 9.4 | 13.6 | 1 | 1 | cd-3, id-3 | both nat |
| | | 20.3 | 12.4 | 15.7 | | | | |
| | | 20.2 | 8.5 | 14.0 | 1 | | 3 | nat |
| | | 21.2 | 9.5 | 12.8 | | 1 | 1 | mur |
| | | 23.8 | 11.4 | 16.8 | | | | |
| | | 22.5 | 9.1 | 10.9 | | | | |
| | | 21.5 | 11.2 | 15.6 | | | | |
| | | 23.5 | 10.9 | 15.6 | | | | |
| | | 20.5 | 9.6 | 11.7 | | | | |
| | | 14.4 | 5.4 | 10.6 | | | | |
| | | 20.3 | 9.5 | 12.1 | | | | |
| | | 25.1 | 12.1 | 16.8 | | | | |
| | | 25.0 | 10.4 | 18.6 | | | | |
| | | 25.8 | 13.5 | 12.2 | | | | |
| | | 22.6 | 10.4 | 13.9 | | | | |
| | | 25.2 | 11.1 | 13.5 | | | | |
| | | 22.3 | 7.7 | 16.9 | | | | |
| | | 22.5 | 10.3 | 15.0 | | | | |
| | | 21.1 | 10.0 | 12.9 | | 1 | 4 | nat |
| | | 22.7 | 7.5 | 14.6 | | | | |
| | | 24.4 | 11.8 | 15.7 | | | | |
| | | 15.7 | 6.5 | 10.8 | | | | |
| | | 20.2 | 9.7 | 12.5 | | | | |
| | | 23.3 | 15.9 | 12.0 | | | | |
| | | 22.3 | 10.3 | 14.3 | | | | |
| | | 24.3 | 12.3 | 15.9 | | | | |
| | | 22.1 | 8.2 | 13.4 | | | | |
| | | 27.8 | 14.8 | 15.1 | | | | |
| | | 28.1 | 14.4 | 14.5 | | | | |
| | | 25.0 | 9.7 | 15.0 | | 1 | 1 | mur |
| | | 17.7 | 10.8 | 10.9 | | | | |
| | | 31.5 | 15.3 | 15.8 | | | | |
| | | 22.1 | 13.6 | 15.9 | | | | |
| | | 25.5 | 10.7 | 17.3 | | | | |
| | | 27.3 | 10.9 | 18.0 | | | | |
| | | 29.2 | 12.6 | 14.9 | | | | |
| | | 27.1 | 12.6 | 16.5 | | | | |
| | | 23.8 | 11.4 | 14.9 | | | | |
| | | 20.0 | 8.9 | 12.2 | 1 | | 3 | nat |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Bermont Fm. | *C. convexa* | 24.6 | 9.7 | 14.9 | | | | |
| Loxahatchee, FL | | 23.6 | 11.2 | 13.4 | | | | |
| | | 25.1 | 10.2 | 17.9 | | | | |
| | | 24.3 | 11.0 | 14.5 | | | | |
| | | 20.6 | 9.3 | 12.3 | | | | |
| | | 21.6 | 7.8 | 12.9 | | 1 | 1 | mur |
| | | **24.2** | **11.1** | **15.1** | | | | |
| | | | | | | | | |
| | *C. maculosa* | 22.5 | 7.6 | 14.8 | | 1 | 3 | nat |
| | | 26.1 | 10.4 | 20.3 | | | | |
| | | 25.2 | 10.0 | 17.2 | | | | |
| | | 18.8 | 9.6 | 13.0 | | | | |
| | | 22.9 | 12.5 | 13.3 | | 1 | 3 | mur |
| | | 30.6 | 11.2 | 19.9 | 1 | 2 | id-1,1; cd-2 | all nat |
| | | 25.0 | 10.7 | 15.7 | | | | |
| | | 18.2 | 6.0 | 13.1 | | 1 | 3 | nat |
| | | 26.8 | 12.9 | 19.7 | | | | |
| | | 23.5 | 9.8 | 15.8 | | | | |
| | | 27.4 | 10.1 | 19.8 | | | | |
| | | 29.8 | 12.1 | 21.0 | | | | |
| | | 22.6 | 7.8 | 15.9 | 2 | | 3,4 | both mur |
| | | 21.9 | 8.3 | 13.9 | | | | |
| | | 18.3 | 8.1 | 13.3 | | | | |
| | | 18.1 | 6.6 | 13.5 | | | | |
| | | 17.8 | 5.8 | 10.2 | | | | |
| | | 34.0 | 11.9 | 23.0 | | | | |
| | | 17.9 | 5.4 | 11.8 | | 1 | 3 | mur |
| | | 28.1 | 10.2 | 18.6 | | | | |
| | | 26.1 | 9.2 | 17.4 | | | | |
| | | 20.8 | 7.9 | 15.1 | | | | |
| | | 25.3 | 11.1 | 14.8 | | | | |
| | | 21.9 | 8.1 | 13.3 | | 1 | 1 | mur |
| | | 21.3 | 7.5 | 14.6 | | | | |
| | | 15.3 | 5.0 | 11.3 | | | | |
| | | 23.8 | 9.0 | 16.6 | | | | |
| | | 24.6 | 10.9 | 19.0 | | | | |
| | | 26.0 | 11.0 | 19.2 | | | | |
| | | 26.2 | 10.2 | 17.3 | | | | |
| | | 13.7 | 4.4 | 8.0 | | | | |
| | | 20.4 | 8.9 | 14.8 | 1 | | 3 | nat |
| | | 18.0 | 7.5 | 15.0 | | | | |
| | | 21.6 | 9.3 | 17.9 | | | | |
| | | 23.0 | 8.4 | 15.1 | | | | |
| | | 33.8 | 12.7 | 20.9 | | | | |
| | | 31.3 | 10.8 | 22.7 | | | | |
| | | 30.9 | 11.6 | 20.8 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Bermont Fm. | *C. maculosa* | 20.5 | 7.8 | 13.7 | | | | |
| Loxahatchee, FL | | 20.5 | 8.4 | 14.7 | | | | |
| | | 22.1 | 8.1 | 15.0 | | | | |
| | | 28.5 | 9.1 | 20.7 | | | | |
| | | 27.2 | 10.1 | 17.0 | | | | |
| | | 23.4 | 9.3 | 14.7 | | | | |
| | | 20.9 | 6.7 | 11.2 | | | | |
| | | 23.7 | 8.8 | 15.6 | | | | |
| | | 20.1 | 6.4 | 14.4 | | | | |
| | | 18.6 | 6.8 | 13.4 | | | | |
| | | 22.7 | 5.3 | 17.3 | | | | |
| | | 25.6 | 10.3 | 15.4 | | | | |
| | | 24.4 | 10.9 | 17.8 | | | | |
| | | 18.8 | 8.7 | 13.7 | 1 | 1 | cd-3, id-3 | both nat |
| | | 20.6 | 8.3 | 14.5 | | | | |
| | | 14.5 | 3.8 | 11.2 | | | | |
| | | 24.8 | 11.9 | 16.7 | | | | |
| | | **23.2** | **8.9** | **15.9** | | | | |
| | | | | | | | | |
| | *C. aculeata* | 25.0 | 12.3 | 18.2 | | | | |
| | | 25.7 | 10.6 | 18.7 | | | | |
| | | 27.5 | 12.4 | 19.1 | | | | |
| | | 28.8 | 8.9 | 21.3 | | | | |
| | | 23.5 | 6.9 | 18.8 | | | | |
| | | 22.4 | 6.3 | 19.1 | | | | |
| | | 21.3 | 9.2 | 15.3 | | | | |
| | | 24.5 | 8.7 | 19.4 | | | | |
| | | 20.5 | 9.0 | 17.2 | | 1 | 4 | nat |
| | | 24.6 | 9.9 | 20.0 | | | | |
| | | 24.5 | 9.2 | 15.9 | | | | |
| | | 27.1 | 12.8 | 22.6 | | | | |
| | | 22.1 | 11.2 | 14.3 | | | | |
| | | 18.4 | 6.7 | 14.1 | | | | |
| | | 14.9 | 6.4 | 12.1 | | | | |
| | | 22.9 | 9.0 | 17.9 | | | | |
| | | 24.0 | 9.5 | 18.0 | | 1 | 4 | mur |
| | | 12.4 | 5.5 | 8.8 | 1 | | 1 | mur |
| | | 19.1 | 8.0 | 16.4 | | | | |
| | | 21.7 | 11.4 | 15.3 | | 1 | 1 | mur |
| | | 22.3 | 9.6 | 15.2 | | | | |
| | | 24.5 | 9.6 | 18.5 | | | | |
| | | 24.0 | 11.1 | 17.5 | | | | |
| | | 22.0 | 9.6 | 14.6 | | | | |
| | | 14.2 | 4.4 | 9.9 | | | | |
| | | 20.6 | 8.5 | 15.4 | | | | |
| | | 16.0 | 6.0 | 11.6 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Bermont Fm. | *C. aculeata* | 19.0 | 8.2 | 14.1 | | | | |
| Loxahatchee, FL | | 21.8 | 9.7 | 18.1 | | | | |
| | | 23.8 | 9.5 | 19.4 | | | | |
| | | 13.5 | 4.5 | 9.8 | | | | |
| | | 25.6 | 8.9 | 18.2 | | | | |
| | | 15.3 | 5.7 | 11.8 | | | | |
| | | 21.0 | 6.4 | 15.3 | | | | |
| | | 21.8 | 9.1 | 16.4 | | | | |
| | | 22.3 | 10.2 | 16.2 | | | | |
| | | 17.9 | 4.4 | 11.7 | 1 | 2 | id-1,3; cd-3 | id-mur, cd-nat |
| | | 15.6 | 6.1 | 13.3 | 1 | | 3 | mur |
| | | 18.2 | 8.0 | 12.8 | | | | |
| | | 24.4 | 12.9 | 16.3 | 1 | | 1 | nat |
| | | 19.3 | 7.6 | 14.9 | | | | |
| | | 23.3 | 9.5 | 17.0 | | | | |
| | | 17.7 | 8.0 | 12.1 | | | | |
| | | 18.8 | 5.8 | 15.8 | | | | |
| | | 18.4 | 7.6 | 14.7 | | | | |
| | | 24.0 | 10.2 | 20.2 | | | | |
| | | 28.0 | 10.4 | 20.8 | 1 | | 1 | mur |
| | | 18.1 | 6.7 | 14.2 | | | | |
| | | 23.6 | 10.4 | 18.3 | 1 | | 3 | nat |
| | | 12.9 | 5.7 | 10.8 | | | | |
| | | 19.9 | 9.6 | 15.9 | | | | |
| | | 16.7 | 6.6 | 12.9 | | | | |
| | | 13.9 | 3.5 | 11.4 | | | | |
| | | 10.3 | 3.6 | 8.1 | | | | |
| | | 17.0 | 7.4 | 14.8 | | | | |
| | | 18.1 | 8.8 | 14.4 | | | | |
| | | 17.1 | 4.9 | 10.9 | | | | |
| | | 19.0 | 8.6 | 14.2 | | | | |
| | | 19.2 | 8.5 | 15.5 | | | | |
| | | **20.5** | **8.3** | **15.5** | | | | |
| | | | | | | | | |
| Bermont Fm. | *C. aculeata* | 22.2 | 10.9 | 16.5 | | | | |
| Longan Lake, FL | | 23.4 | 8.3 | 16.5 | | | | |
| | | 24.7 | 11.4 | 18.2 | | | | |
| | | 28.3 | 13.4 | 18.7 | | | | |
| | | 21.6 | 10.0 | 15.3 | | | | |
| | | 21.7 | 8.0 | 16.0 | | | | |
| | | 19.6 | 9.5 | 13.6 | | | | |
| | | 18.6 | 6.7 | 14.4 | | | | |
| | | 17.5 | 7.9 | 13.1 | | | | |
| | | 22.4 | 8.5 | 17.4 | | | | |
| | | 19.3 | 8.7 | 13.2 | | | | |
| | | 23.1 | 10.8 | 17.2 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Bermont Fm. | *C. aculeata* | 18.7 | 8.4 | 13.3 | | | | |
| Longan Lake, FL | | 23.0 | 7.7 | 17.4 | | | | |
| | | 21.8 | 8.4 | 11.7 | | | | |
| | | 23.4 | 10.6 | 14.7 | | | | |
| | | 16.5 | 7.3 | 14.3 | | | | |
| | | 24.2 | 11.2 | 18.0 | | | | |
| | | 20.3 | 6.5 | 16.1 | | | | |
| | | 15.9 | 7.6 | 13.2 | | | | |
| | | 26.7 | 7.9 | 19.5 | | | | |
| | | 21.6 | 9.6 | 15.7 | | | | |
| | | 19.3 | 7.1 | 14.9 | | | | |
| | | 22.0 | 8.7 | 13.3 | | | | |
| | | 18.3 | 6.1 | 14.4 | | | | |
| | | 19.6 | 6.4 | 13.1 | | | | |
| | | 16.0 | 7.8 | 12.2 | | | | |
| | | 17.0 | 7.3 | 12.1 | | | | |
| | | 20.6 | 8.5 | 15.3 | | | | |
| | | 18.0 | 7.7 | 12.7 | | | | |
| | | 21.1 | 8.6 | 15.8 | | | | |
| | | 20.2 | 5.4 | 11.7 | | | | |
| | | 22.4 | 8.8 | 17.2 | | | | |
| | | 18.2 | 6.9 | 13.8 | | | | |
| | | 21.0 | 9.5 | 14.7 | | | | |
| | | 18.3 | 5.9 | 12.6 | | | | |
| | | 22.0 | 8.7 | 17.0 | | | | |
| | | 20.5 | 8.3 | 14.0 | | | | |
| | | 11.6 | 3.4 | 8.1 | | | | |
| | | 13.7 | 4.4 | 11.0 | | | | |
| | | 20.8 | 8.9 | 15.5 | | | | |
| | | 13.9 | 4.7 | 8.8 | 2 | | 1,3 | nat |
| | | 17.3 | 5.1 | 12.5 | | | | |
| | | **20.1** | **8.1** | **14.5** | | | | |
| | | | | | | | | |
| | *C. maculosa* | 33.4 | 14.4 | 26.2 | | | | |
| | | 18.4 | 5.9 | 13.2 | | | | |
| | | 25.4 | 9.4 | 17.6 | | 1 | 3 | mur |
| | | 30.3 | 8.2 | 20.2 | | | | |
| | | 25.8 | 9.9 | 19.3 | | | | |
| | | 23.3 | 6.5 | 18.1 | | | | |
| | | 20.8 | 6.3 | 15.3 | | | | |
| | | 30.0 | 9.2 | 22.3 | | | | |
| | | 27.2 | 11.0 | 19.8 | | | | |
| | | 26.0 | 6.6 | 20.1 | | | | |
| | | 22.4 | 7.5 | 16.2 | | | | |
| | | 18.8 | 5.1 | 13.1 | | | | |
| | | 25.0 | 6.6 | 16.5 | | | | |

| Strat. Interval | Species | L | H | W | CD | ID | Dr. Loc. | Dr. Type |
|---|---|---|---|---|---|---|---|---|
| Bermont Fm. | *C. maculosa* | 18.1 | 4.9 | 12.6 | | | | |
| Longan Lake, FL | | 12.9 | 3.7 | 7.9 | | | | |
| | | 14.7 | 4.2 | 10.2 | | | | |
| | | 19.4 | 6.5 | 11.6 | | | | |
| | | 15.8 | 3.8 | 9.8 | | | | |
| | | 15.9 | 6.2 | 9.0 | | | | |
| | | 16.6 | 4.9 | 10.8 | | | | |
| | | 12.6 | 2.6 | 8.0 | | | | |
| | | **21.6** | **6.8** | **15.1** | | | | |
| | | | | | | | | |
| | *C. plana* | **22.7** | **1.8** | **17.1** | | | | |
| | | | | | | | | |
| | *C. fornicata* | 27.0 | 12.9 | 17.4 | | | | |
| | | 23.5 | 11.5 | 11.0 | | | | |
| | | 46.4 | 24.2 | 16.4 | | | | |
| | | 30.5 | 11.8 | 16.4 | | 1 | 3 | mur |
| | | 28.0 | 11.1 | 14.6 | | | | |
| | | 29.4 | 15.5 | 21.9 | | | | |
| | | 28.7 | 16.8 | 17.3 | | | | |
| | | 24.7 | 10.3 | 13.6 | 1 | | 4 | mur |
| | | 22.8 | 10.2 | 11.3 | | 2 | 1 | mur |
| | | 23.0 | 11.1 | 12.8 | 1 | | 3 | nat |
| | | 21.7 | 6.8 | 14.8 | 1 | | 3 | nat |
| | | **27.8** | **12.9** | **15.2** | | | | |
| | | | | | | | | |
| | *C. convexa* | 31.3 | 13.2 | 18.6 | | | | |
| | | 32.8 | 12.1 | 21.1 | | | | |
| | | 20.4 | 7.2 | 14.3 | | | | |
| | | 26.0 | 10.3 | 16.7 | | | | |
| | | 25.7 | 8.8 | 17.9 | | | | |
| | | 25.1 | 10.8 | 17.1 | | | | |
| | | 24.5 | 9.3 | 17.4 | | | | |
| | | 24.3 | 9.1 | 16.9 | | | | |
| | | 22.9 | 6.8 | 14.6 | | | | |
| | | 18.4 | 5.0 | 10.3 | | | | |
| | | 23.7 | 6.7 | 15.0 | | | | |
| | | 27.2 | 10.0 | 18.4 | | | | |
| | | 25.0 | 8.7 | 16.2 | | | | |
| | | 24.9 | 8.9 | 16.8 | | 1 | 3 | mur |
| | | 20.5 | 8.2 | 14.5 | | | | |
| | | **24.8** | **9.0** | **16.4** | | | | |

Abbreviations are as follows: Strat. Interval=Stratigraphic Interval; L=shell length; H=shell height; W=shell width (numbers in bold are average L, H, & W for each species at that locality); CD=#complete drillholes; ID=#incomplete drillholes; Dr. Loc.=drillhole location (sectors 1-5); Dr. Type=type of drillhole (muricid (mur) or naticid (nat) in origin).